





# ENVIRONMENTAL & WATER QUALITY OPERATIONAL STUDIES

TECHNICAL REPORT E-83-15

# U. S. ARMY CORPS OF ENGINEERS RESERVOIR MODEL, CE-QUAL-R1

by

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This report supplies information about, and literature values for, many of the coefficients needed for the U. S. Army Corps of Engineers Reservoir Model, CE-QUAL-Rl. Most of the information presented concerns biological processes of gross production, ingestion, respiration, mortality, and decomposition. Coefficients specified are suitable for the algorithms described in the

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#### PREFACE

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The study was conducted under the direct supervision of Mr. Aaron Stein, Acting Chief, WQMG, and under the general supervision of Mr. Donald L. Robey, Chief, Ecosystem Research and Simulation Division, and Dr. John Harrison, Chief, EL, WES. Program Manager of EWQOS was Dr. Jerome L. Mahloch, EL.

Commander and Director of WES during this study and the preparation of this report was Col. Tilford C. Creel, CE. Technical director was Mr. F. R. Brown.

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# CONTENTS

|                                   | Page          |
|-----------------------------------|---------------|
| PREFACE                           | 1             |
| LIST OF TABLES                    | $\frac{-}{4}$ |
| PART I: INTRODUCTION              | 6             |
|                                   | _             |
| Background                        | 6<br>6        |
| Purpose                           | 6             |
| PART II: COEFFICIENTS             | 10            |
| Coefficient Types                 | 10            |
| Physiological Processes           | 11            |
| Light Extinction                  | 12            |
| EXCO                              | 13            |
| EXTINS and EXTINP                 | 15            |
| Phytoplankton                     | 18            |
| TPRESP                            | 18            |
| TPMAX                             | 20            |
| TSETL                             | 28            |
| PS2PO4                            | 32            |
| PS2N                              | 34            |
| PS2CO2                            | 38            |
| PS2L                              | 40            |
| ALGT1, ALGT2, ALGT3, ALGT4        | 42            |
| Zooplankton                       | 44            |
| TZMAX                             | 44            |
| TZMORT                            | 46            |
| ZEFFIC                            | 47            |
| PREF1, PREF2, PREF3               | 49            |
| TZRESP                            | 51            |
| ZS2P                              | 53            |
| ZOOT1, ZOOT2, ZOOT3, ZOOT4        | 53            |
| Benthos                           | 56            |
| TBMAX                             | 56            |
| TBMORT                            | 59            |
| BEFFIC                            | 59            |
| BS2SED                            | 60            |
| TBRESP                            | 60            |
| BENT1, BENT2, BENT3, BENT4        | 62            |
| Fish                              | 62            |
| TFMAX                             | 63            |
| FS2BEN, FS2ZOO, FS2FSH            | 63            |
| F2ALG, F2DET, F2ZOO, F3BEN, F3SED | 64            |
| FSHT1, FSHT2, FSHT3, FSHT4        | 66            |
| FEFFIC                            | 69            |
| TFMORT                            | 69            |
| TERESP                            | 70            |

| Ot   | her Co | oefficients     | 71 |
|------|--------|-----------------|----|
|      | TDSET  | TL              | 71 |
|      | DETT.  | l, DETT2        | 72 |
|      | TDOMI  | DK              | 73 |
|      | TNH3I  | DK              | 75 |
|      | TNO2I  | DK              | 77 |
|      | TDETI  | DK              | 77 |
|      | TCOLI  | DK              | 80 |
|      | TSEDI  | DK              | 84 |
|      | DOMT:  | 1, DOMT2        | 84 |
|      | NH3T.  | 1, NH3T2        | 85 |
|      | NO2T.  | 1, NO2T2        | 86 |
|      | TSSET  | TL              | 86 |
|      | Qloco  | OL              | 86 |
| PART | III:   | RECOMMENDATIONS | 87 |
| REFE | RENCES |                 | 88 |

# LIST OF TABLES

| $\underline{\text{No.}}$ |   | Page |
|--------------------------|---|------|
| 1                        | Alphabetical listing of the coefficients in this report   | 8    |
| 2                        | Extinction coefficients for water $(1/m)$   | 14   |
| 3                        | Self-shading coefficients due to particulate matter (1/m*mg/L)  | 17   |
| 4                        | Phytoplankton dark respiration rates (1/day)  | 20   |
| 5                        | Gross production rates of phytoplankton (1/day)   | 25   |
| 6                        | Phytoplankton settling rates (m/day)  | 30   |
| 7                        | Phytoplankton half-saturation coefficients for P limitation (mg/L)  | 33   |
| 8                        | Phytoplankton half-saturation coefficients for N limitation (mg/L)  | 36   |
| 9                        | Phytoplankton half-saturation coefficients for CO2 limitation (mg/L)  | 39   |
| 10                       | Phytoplankton half-saturation coefficients for light limitation (kcal/m <sup>2</sup> /hr)   | 41   |
| 11                       | Temperature coefficients for phytoplankton (°C)   | 43   |
| 12                       | Maximum ingestion rates for zooplankton (1/day)   | 45   |
| 13                       | Zooplankton mortality rates (1/day)   | 46   |
| 14                       | Zooplankton assimilation efficiency coefficients (dimensionless)  | 48   |
| 15                       | Food preference factors of zooplankton (dimensionless)  | 50   |
| 16                       | Zooplankton maximum respiration rates (1/day)   | 52   |
| 17                       | Zooplankton half-saturation coefficients (mg/L)   | 53   |
| 18                       | Zooplankton temperature coefficients (°C)   | 54   |
| 19                       | Acclimation temperature, upper and lower lethal temperature, and the temperature range for a constant maximum grazing rate for zooplankton exposed to rapid temperature stress (°C) | 55   |
| 20                       | Daily ration of benthic organisms (1/day)   | 57   |
| 21                       | Benthos maximum ingestion rates (1/day)   | 58   |
| 22                       | Benthos assimilation efficiencies (dimensionless)   | 59   |

| No. |   | Page |
|-----|---|------|
| 23  | Maximum respiration rates for benthos (1/day)                                 | 61   |
| 24  | Temperature coefficients for benthos metabolism (°C)                          | 62   |
| 25  | Estimated half-saturation coefficients for fish growth (mg/L)                 | 64   |
| 26  | Fish food expressed as a fraction of the diet                                 | 65   |
| 27  | Temperature coefficients for fish ingestion (°C)                              | 67   |
| 28  | Assimilation efficiencies of fish (dimensionless)                             | 69   |
| 29  | Fish nonpredatory mortality rates (1/day)                                     | 70   |
| 30  | Fish maximum respiration rates (1/day)  | 71   |
| 31  | Detritus settling velocities (m/day)  | 72   |
| 32  | Temperature coefficients for decomposition (°C)                               | 73   |
| 33  | DOM decay rates (1/day)   | 75   |
| 34  | Ammonia oxidation rates (1/day)   | 76   |
| 35  | Detritus decay rates (1/day)  | 80   |
| 36  | Coliform and fecal streptococcus decay rates (1/day)                          | 82   |
| 37  | Freshwater die-off rates of coliform bacteria measured <u>in situ</u> (1/day) | 83   |
| 38  | Temperature coefficients for DOM decay (°C)                                   | 85   |
| 39  | Temperature coefficients for ammonia oxidation (°C)                           | 85   |

# COEFFICIENTS FOR USE IN THE U. S. ARMY CORPS OF ENGINEERS RESERVOIR MODEL, CE-QUAL-R1

#### PART I: INTRODUCTION

# Background

1. A numerical one-dimensional model (CE-QUAL-R1) of reservoir water quality is being developed as part of the Environmental and Water Quality Operational Studies (EWQOS). A User's Manual (Environmental Laboratory 1982), which describes the model and lists the data required, is available from the U. S. Army Engineer Waterways Experiment Station (WES). One of the major types of input to the model is a set of coefficients used in equations which describe rates of change for various water quality variables. Although a description of the coefficients is included in the User's Manual, no values are supplied for many of them. Most of these deal with biological processes which are extremely difficult, and very costly, to measure; in fact, for a pre-impoundment study, many coefficients cannot be measured. For these reasons, users of CE-QUAL-R1 will have to use coefficient estimates found in the literature.

#### Purpose

2. The purpose of this report is to aid the users of CE-QUAL-Rl by supplying information about, and values for, many of the coefficients needed for use of the model. Table 1 lists those coefficients for which information is supplied in this report. The coefficients presented are

suitable for the version of the model described in the User's Manual (Environmental Laboratory 1982). Neither the information concerning coefficient measurements nor the coefficient values listed should be considered to represent an exhaustive search of the literature. In many cases, the parameter values found in the literature were inappropriate to use in the model because of (a) the lack of information necessary to convert the value to the proper units or (b) improper experimental design. Therefore, this report includes literature values for experiments that were already in appropriate form for use in CE-QUAL-R1 or were readily transformable.

3. Although parameter values for a given coefficient may range over several orders of magnitude, it was felt inappropriate to recommend a single value for a parameter. Instead, experimentally determined values are presented to provide the user with a range of values.

Table 1

Alphabetical listing of coefficients in this report

|             |      | PAGE NUMBE | rs*                                   |
|-------------|------|------------|---------------------------------------|
| COEFFICIENT | THIS | REPORT     | USER'S MANUAL                         |
| ALGT1       |      | 42         | 193,194                               |
| ALGT2       |      | 42         | 193,194                               |
| ALGT3       |      | 42         | 193,194                               |
| ALGT4       |      | 42         | 193,194                               |
| BEFFIC      |      | 59         | 197                                   |
| BENTl       |      | 62         | 198                                   |
| BENT2       |      | 62         | 198                                   |
| BENT3       |      | 62         | 198                                   |
| BENT4       |      | 62         | 198                                   |
| BS2SED      |      | 60         | 197                                   |
| DETT1       |      | 72         | 199                                   |
| DETT2       |      | 72         | 199                                   |
| DOMT1       |      | 84         | 209                                   |
| DOMT2       |      | 84         | 209                                   |
| EXCO        |      | 13         | 182                                   |
| EXTINP      |      | 15         | 187                                   |
| EXTINS      |      | 15         | 182                                   |
| FEFFIC      |      | 69         | 203,204,205                           |
| FSHT1       |      | 66         | 203,204,205                           |
| FSHT2       |      | 66         | 203,204,205                           |
| FSHT3       |      | 66         | 203,204,205                           |
| FSHT4       |      | 66         | 203,204,205                           |
| FS2BEN      |      | 63         | 201                                   |
| FS2FSH      |      | 63         | 201                                   |
| FS2ZOO      |      | 63         | 201                                   |
| F2ALG       |      | 64         | 202                                   |
| F2DET       |      | 64         | 202                                   |
| F2ZOO       |      | 64         | 202                                   |
| F3BEN       |      | 64         | 202                                   |
| F3SED       |      | 64         | 202                                   |
| NH3T1       |      | 85         | 210                                   |
| NH3T2       |      | 85         | 210                                   |
| NO2T1       |      | 86         | 211                                   |
| NO2T2       |      | 86         | 211                                   |
| PREF1       |      | 49         | 195                                   |
| PREF2       |      | 49         | 195                                   |
|             | (Co  | ntinued)   | · · · · · · · · · · · · · · · · · · · |

<sup>\*</sup>The page numbers reflect a cross-reference between this document and the User's Manual (Environmental Laboratory 1982).

Table 1 (Concluded)

# PAGE NUMBERS\*

| COEFFICIENT | THIS REPORT | USER'S MANUAL |
|-------------|-------------|---------------|
| PREF3       | 49          | 195           |
| PS2CO2      | 38          | 191,192       |
| PS2L        | 40          | 191,192 .     |
| PS2N        | 34          | 190,192       |
| PS2PO4      | 32          | 190,192       |
| QlocoL      | 86          | 213           |
| TBMAX       | 56          | 197           |
| TBMORT      | 59          | 197           |
| TBRESP      | 60          | 197           |
| TCOLDK      | 80          | 207           |
| TDETDK      | 77          | 207           |
| TDOMDK      | 73          | 207           |
| TDSETL      | 71          | 199           |
| TFMAX       | 63          | 201           |
| TFMORT      | 69          | 203,204,205   |
| TFRESP      | 70          | 203,204,205   |
| TNH3DK      | 75          | 207           |
| TNO2DK      | 77          | 207           |
| TPMAX       | 20          | 189,192       |
| TPRESP      | 18          | 187           |
| TSEDDK      | 84          | 207           |
| TSETL       | 28          | 212           |
| TSSETL      | 86          | 189,192       |
| TZMAX       | 44          | 195           |
| TZMORT      | 46          | 195           |
| TZRESP      | 51          | 195           |
| ZEFFIC      | 47          | 195           |
| ZOOT1       | 53          | 196           |
| ZOOT2       | 53          | 196           |
| ZOOT3       | 53          | 196           |
| ZOOT4       | 53          | 196           |
| ZS2P        | 53          | 196           |
|             | 33          | 100           |

#### PART II: COEFFICIENTS

## Coefficient Types

4. For those coefficients that are involved in equations as rates of change, the user <u>must</u> supply values that are appropriate to continuous exponential functions. These values should be appropriate for the equation:

$$X(t) = X_{O} \exp(K_{C}^{*}t)$$
 (1)

where

X(t) = final condition

 $X_{o} = initial condition$ 

K<sub>c</sub> = coefficient in units of 1/day in continuous
form

t = time in days

5. For those coefficients that are negative (e.g., mortality rate), the negative sign is introduced internally by the model. If values are reported in the discrete form suitable for the equation

$$X(t) = X_0 (1+K_{\bar{d}}) **n$$
 (2)

where

 $K_d$  = coefficient in units of l/day in discrete form

n = the number of time steps in days
the coefficient must be transformed. If the user has
coefficients in the discrete form in units of 1/day, they
can be transformed to the proper continuous form by using
the following relationship:

$$K_{c} = \ln (1 + K_{d}) \tag{3}$$

For a detailed explanation of the type of coefficients used by CE-QUAL-R1, please refer to the User's Manual, pages 41 through 47 (Environmental Laboratory 1982). Values included in this report are in the continuous form. This entailed transforming values for those citations that

were reported in the discrete form; transformations of units to the form used by the model were also necessary.

# Physiological Processes

- 6. For zooplankton, fish, and benthos, the physiological processes modeled are ingestion, respiration, and assimilation efficiency. The units for ingestion are 1/day. Assimilation efficiency is dimensionless and is multiplied by ingestion to account for the assimilation rate. In the literature, ingestion (I) or consumption is equal to assimilation (A) + egestion (E). The amount assimilated may be separated into (a) that amount respired (R) and (b) growth (G). The products of growth may be separated into excretion (X), predatory mortality (PM), nonpredatory mortality (NM), exuviae (V), secretion (S), eggs or young (Y), harvest (H), and the change in weight (WT).
- 7. In CE-QUAL-R1 predictions are made regarding WT. In the literature it usually equals

$$WT = I - E - R - X - PM - NM - V - S - Y - H \tag{4}$$

Ingestion, respiration, predatory mortality, nonpredatory mortality, and harvest are explicitly modeled. Egestion is calculated using ingestion and the assimilation efficiency. Eggs or young are not considered lost in the model and are not included in the equation. Excretion, exuviae, and secretion are considered as part of the nonpredatory mortality term. Values for growth should be used with caution. Model users must know exactly what is included in the growth term so that correct coefficient estimates can be made.

8. The rates used in the model represent the maximum rate for each process under conditions normally

found in reservoirs. These maximum rates are scaled down in the model due to predicted conditions such as temperature, nutrient, or food concentrations. Values found in the literature for rates are often measured at a set of specific conditions and may not represent a true maximum rate. Values found in this report may not necessarily be maximum rates, but the authors felt that the information may still be of use in setting coefficients. The ingestion rate must be greater than the combined mortality and respiration rates divided by the assimilation efficiency.

9. Data input and coefficient selection are discussed in detail. Guidance will be given with respect to how the data item is used in the model and how the data item can be calculated or determined. Values for the coefficients are also given in tables based upon results from laboratory and in situ experimental results. With careful specification of coefficient values, calibration efforts can be held to a minimum.

## Light Extinction

10. Solar radiation is distributed vertically in the water column in subroutine HEAT (which is called from subroutine MIXING). The distribution is due in part to the absorption of light by water, including dissolved substances, and by absorption by particulate organic and inorganic materials. Care must be taken when estimating or measuring extinction coefficients, for the same coefficient may have a different meaning depending on whether it is used in CE-QUAL-Rl or CE-THERM-Rl. Two extinction coefficients are used in CE-THERM-Rl: EXCO and EXTINS; EXTINP is used only in CE-QUAL-Rl.

## EXCO

11. EXCO is the extinction coefficient for water, including dissolved substances (1/m). It can be estimated from the equation (Williams et al. 1981)

$$EXCO = 1.1*Z**(-0.73)$$
 (5)

given the Secchi depth (Z) in meters, or it can be measured directly with a photometer using the Beers-Lambert Law

$$EXCO = (ln I-ln I_{7})/Z$$
 (6)

where

I = irradiance at water surface

However, in situ measurements for EXCO are likely to overestimate the extinction coefficient because it includes extinction due to detritus, phytoplankton, zooplankton, and inorganic suspended solids. Thus, the manual carefully states on p. 182 that the calculated value of EXCO should reflect the maximum light penetration (i.e., the maximum Secchi depth). This should minimize the overestimation problem. In CE-QUAL-R1 and CE-THERM-R1, self-shading due to these components is handled separately.

12. The light extinction coefficient for an ultra-oligotrophic to oligotrophic lake ranges from 0.03 to 1.0/m; for mesotrophic lakes the figures are from 0.1 to 2.0/m; for eutrophic lakes, from 0.5 to 4.0/m; and for dystrophic lakes, from 1.0 to 4.0/m (Likens 1975). The extinction coefficient of monochromatic light by a 1-m column of distilled water ranges from 0.0255 at 380 nm, 0.0054 at 460 nm, 0.078 at 580 nm, 0.455 at 680 nm, to 2.42 at 820 nm (Hutchinson 1957). Other values are given in Table 2 for photosynthetically active radiation (PAR) and other wavelengths.

Table 2
Extinction coefficients for Water (1/m)

| SITE   | DESCRIPTION                           | EXCO      | REFERENCE    |
|--|---------------------------------------|-----------|--------------|
| Lake Tahoe, California                         | oligotrophic                          | 0.2       | Wetzel 1975  |
| Wintergreen Lake, Michigan                     | eutrophic                             | 0.46-1.68 | Wetzel 1975  |
| Crystal Lake, Wisconsin<br>Crater Lake, Oregon | oligotrophic<br>oligotrophic,         | 0.2       | Wetzel 1975  |
| • •  | almost pure, blue                     | 0.18      | Spence 1981  |
| Loch Borralie, Scotland                        | calcareous water,                     |           |              |
| •  | blue green                            | 0.34      | Spence 1981  |
| Neusiedlersee, Austria                         | turbid water,                         |           | •            |
|  | sediment colored                      | 3.31      | Spence 1981  |
| Loch Unagan, Scotland<br>Black Loch, Scotland  | yellow substances<br>brown substances | 0.93      | Spence 1981  |
|  | (peaty)                               | 1.53      | Spence 1981  |
| Loch Leven, Scotland                           | turbid, dense                         |           | -            |
|  | phytoplankton                         | 2.58      | Spence 1981  |
| Lake Paajarvi, Finland                         | brown-stained                         | 0.7       | Verduin 1982 |
| Highly stained lakes                           | average                               | 4.0       | Wetzel 1975  |

#### EXTINS and EXTINP

- EXTINS is the self-shading coefficient due to particulate inorganic material in both CE-QUAL-R1 and CE-THERM-R1. In CE-THERM-R1, because organic particulate materials are not explicitly modeled, the light attenuation due to these materials must be handled through either EXTINS or EXCO. If the suspended solids (SS) compartment has been incremented in value to include organic as well as inorganic particulates suspended in the water column, then EXTINS (1/m\*mg/L) represents the extinction coefficient for all suspended solids, including inorganic matter, phytoplankton, zooplankton, and suspended detritus. However, if the SS compartment in CE-THERM-Rl does not include organic particulates -i.e., if the magnitude of SS is identical in CE-QUAL-R1 and CE-THERM-R1--then light attenuation by organic matter suspended in the water column cannot be handled by EXTINS. Rather, the value of EXCO must be increased to handle the "extra" attenuation due to phytoplankton, zooplankton, and detritus. In either case, the magnitude of EXTINS should be the same in both models. It should typically be of the same order of magnitude as EXTINP.
- 14. EXTINP is the self-shading coefficient due to organic particulate matter in CE-QUAL-Rl (1/m\*mg/L). The self-shading coefficient represents the decreased light penetration or increased light extinction resulting from phytoplankton, zooplankton, and detritus suspended in the water column. The light extinction coefficient in subroutine HEAT is modified as a function of the concentrations of these three constituents. Most measurements of EXTINP refer only to algal biomass; it is assumed in CE-QUAL-Rl that light extinction due to

zooplankton and detritus is numerically equivalent to that due to phytoplankton. Megard et al. (1980) and Smith and Baker (1978) determined that each microgram per liter of chlorophyll increased the light extinction coefficient by about 0.022 and 0.016/m, respectively. Assuming a ratio of carbon to algal biomass of 0.45 and a carbon/chlorophyll (C/chl) ratio of 50, then algebraically each milligram per liter of algal biomass should increase the light extinction coefficient by about 0.20 to 0.14/m, respectively. The range of C/chl ratios, however, varies from 25-150, resulting in a range of self-shading coefficients from 0.40/m\*mg/L to 0.047/m\*mg/L. Values near 0.10 have previously produced reasonable results (Environmental Laboratory 1982).

Light extinction by algae is computed from in situ light intensity measurements at depth intervals and in situ determinations of chlorophyll a using the modified Lambert-Bouquer Law (Megard et al. 1980). Bannister (1979) extracted chlorophyll from cell suspensions and measured the absorption spectrum to obtain the mean extinction coefficient. Theoretical estimates for attenuation of photosynthetically active radiation by chlorophyll a in algae range between 0.06 and 0.018, depending on the size and chlorophyll content of cells and colonies (Kirk 1975). The extinction coefficient was determined to range between 0.0066 and 0.0205 l/m\*mg/m3 in laboratory analysis (Bannister 1979). Values for self-shading coefficients are given in Table 3. Values shown in this table were originally reported in units of 1/m\*µg chl a/L, and have been converted to units used in CE-QUAL-Rl assuming a C/chl ratio of 50 and a C/biomass ratio of 0.45.

Table 3  $\frac{\text{Self-shading coefficients due to particulate matter}}{(1/\text{m*mg/L})}$ 

| $\underline{\mathtt{TYPE}}$ | COMMENT                       | VALUE | REFERENCE             |
|-----------------------------|-------------------------------|-------|-----------------------|
| Suspensoids                 | average                       | 0.12  | Verduin 1982          |
| Suspensoids                 | Lake Paajarvi,                |       |                       |
|                             | Finland                       | 0.24  | Verduin 1982          |
| Organic matter              | Pacific Ocean                 | 0.047 | Verđuin 1982          |
| Phytoplankton               | Pacific Ocean                 | 0.033 | Verduin 1982          |
| Phytoplankton -             | C/Chl ratio = 120             |       |                       |
| diatoms                     | dry wt/C ratio = 4            | 0.058 | Verduin 1982          |
| Phytoplankton -             | C/Chl ratio = 30              |       |                       |
| diatoms                     | <pre>dry wt/C ratio = 4</pre> | 0.014 | Verduin 1982          |
| Phytoplankton -             | C/Chl ratio = 100             |       |                       |
| greens                      | <pre>dry wt/C ratio = 2</pre> | 0.024 | Verduin 1982          |
| Phytoplankton -             | C/Chl ratio = 30              |       |                       |
| greens                      | <pre>dry wt/C ratio = 2</pre> | 0.007 | Verđuin 1982          |
| Phytoplankton               | Shagawa Lake,                 |       |                       |
|                             | Minnesota                     | 0.03  | Megard et al.<br>1980 |

# Phytoplankton

#### TPRESP

- 16. TPRESP is the maximum phytoplankton respiration rate (1/day). Although two compartments are available to simulate phytoplankton, a single respiration rate coefficient is used and should reflect the composite nature of the species assemblages. TPRESP should include dark respiration and photorespiration. Endogenous or dark respiration (mitochondrial) refers to the oxygen consumption associated primarily with oxidative phosphorylation and which produces carbon dioxide. Photorespiration, commonly referred to as excretion, is the release of dissolved organic matter (glycolate) and carbon dioxide that occurs during light periods; it is the oxygen-sensitive loss of carbon dioxide during photosynthesis, stimulated by an increase in temperature or oxygen concentration (Birmingham et al. 1982).
- 17. Measurement of dark respiration in the light is hampered by the presence of photosynthetic oxygen production and photorespiratory oxygen consumption; this precludes direct measurement in the light using a pO2 electrode. Oxygen consumption in the dark depends on the previous light history in several ways. The duration, spectrum and magnitude of light, as well as other factors, determine the type and amount of photosynthate produced. Subsequent respiration in the dark will be affected by the metabolism of the photosynthate and by certain diel The previous light history thus may affect the dark respiration for many hours after a light-dark transition. Transient phenomena in oxygen exchange also are noted for approximately 10 min after the light-dark

transition. Therefore, determination of oxygen consumption should be made after a 5- to 10-min acclimation to a dark environment. It can be measured polarographically using an oxygen electrode, manometrically, or chemically.

- 18. Respiration rates, in many instances, are expressed as milliters of oxygen consumed per milligram of organism dry weight per hour. Since the model formulation requires units of 1/day, these values must be converted. For values in this report, the method outlined on page 188 of the User's Manual (Environmental Laboratory 1982) was used. In addition, respiration values in Table 4 are in continuous form.
- 19. The amount of excretion of organic matter by phytoplankton is commonly expressed as a percent of photoassimilated carbon. It is measured using <sup>14</sup>C as a tracer in photosynthetic uptake rate studies. After incubation and filtration of the algae, the filtrate is then acidified and either (a) bubbled with air for 2 hr or (b) allowed to stand overnight in a dessicator of sodium hydroxide pellets. Rates of carbon dioxide release in the light are lower than rates of dark respiration (Birmingham et al. 1982). Percent extracellular release (PER) values reported in the literature range from 7 to 50 for natural phytoplankton populations (Nalewajko 1966). Berman (1976) reported PER values of 3 to 32 for natural phytoplankton populations in Lake Kinneret.
- 20. The values given in Table 4 for dark respiration rates are usually determined for a 1-hr time period.

Table 4
Phytoplankton dark respiration rates (1/day)

| SPECIES                                     | TPRESP     | REFERENCE                   |
|---|------------|-----------------------------|
| Mesodinium rubrum<br>Thalassiosira allenii- | 0.05       | Smith 1979                  |
| small cells Thalassiosira allenii-          | 0.14-0.59  | Laws and Wong 1978          |
| large cells                                 | 0.05-0.42  | Laws and Wong 1978          |
| Monochrysis lutheri                         | 0.15-0.32  | Laws and Wong 1978          |
| Dunaliella teriolecta                       | 0.12-0.46  | Laws and Wong 1978          |
| Anabaena variabilis                         | 0.10-0.92  | Collins and Boylen<br>1982a |
| Coscinodiscus excentricus                   | 0.075-0.11 | Riley and von Aux<br>1949   |
| Chlorella pyrenoidosa                       | 0.01-0.03  | Myers and Graham<br>1961    |
| Phytoplankton                               | 0.05-0.10  | Ryther 1954                 |

#### TPMAX

- 21. TPMAX is the maximum gross photosynthetic rate (1/day). CE-QUAL-Rl uses gross production rates to simulate the rate of change of algal biomass through time.
- 22. The physiological processes of phytoplankton that are being modeled are gross production and respiration. Gross production is the total rate of photosynthesis, which includes the storage rate of organic matter by the phytoplankton (net production) plus the organic matter used by phytoplankton in respiration. That is,

gross production = net production + respiration (7)

23. Net production is the organic matter used for other processes such as zooplankton grazing, sinking, excretion, and nonpredatory mortality. Extreme care must be used in estimating these rates because the rates are

often dependent on the experimental design. For example, the maximum growth rate is often used in modeling studies (see, for example, the Preliminary Generalized Computer Program, Water Quality for River-Reservoir Systems, Oct. 1978, U. S. Army Engineer Hydrologic Engineering Center, Davis, Calif.). The respiration rate is subtracted from the maximum growth rate in order to predict a new mass. However, the values of growth found in the literature are most equivalent to net production in the above equation and have already accounted for respiration; in other words, the model may predict low phytoplankton values because respiration is being accounted for twice. If growth is measured as the difference in mass between two points in time, it must be realized that algae may have been lost to grazing, sinking, etc. Also, the true growth figure is actually higher than reported.

- 24. Values are often reported as "production" without mention as to whether the figures represent gross or net production, and the reader may have to evaluate the experimental design to determine the correct value.
- 25. There are four general methods used to measure phytoplankton primary productivity (Janik et al. 1981). These involve the measurement of (a) changes in the oxygen content of water, (b) changes in the carbon dioxide content of water, (c) incorporation of <sup>14</sup>carbon tracers into the organic matter of phytoplankton, and (d) measures of chlorophyll. Readers should refer to Janik et al. (1981) to gain insight into the problems associated with the four methods. For example, the <sup>14</sup>carbon technique gives a measurement which is between net and gross production, depending on the length of the experiment (Whittaker 1975).
- 26. The most frequently used method for measuring primary production by phytoplankton has been photosynthetic

oxygen evolution and <sup>14</sup>C uptake. The light- and dark-bottle <sup>14</sup>C technique of Steemann-Nielsen (1952) requires the lowering of pairs of bottles injected with H<sup>14</sup>CO3 to fixed depths in the water column for time periods of 1-5 hrs or by incubating the bottles under known conditions of light and temperature.

27. Under optimal conditions, a culture grows so that the rate of addition of cells is proportional to the number present (i.e., exponential growth). Cells divide in a characteristic time called the division, generation, or doubling time. Population growth follows the solution to the equation

$$dN/dt = k*N$$
 (8)

where

N = the number or concentration of cells in the culture

t = the time

k = the growth constant - (1/t)

The solution to this equation is

$$k = \ln(N/N_0)/(t-t_0)$$
 (9)

Subscripts denote values at a known initial time, and ln indicates natural logarithms.

28. The growth constant k is the number of the logarithm-to-the-base-e units of increase per day. Growth rate is sometimes expressed as logarithm-to-base-10 units of increase per day,  $k_{10}$ ; or as logarithm-to-base-2 units per day,  $k_{2}$ , where

$$k_{10} = log(N/N_0)/(t-t_0)$$
 (10)

$$k_2 = \log_2 (N/N_0)/(t-t_0)$$
 (11)

Conversions among the expressions are as follows: let

k = growth rate measured in ln units

 $k_{10}$  = growth rate measured in  $log_{10}$  units

 $k_2$  = growth rate measured in  $\log_2$  units Now let an algal population of interest double in one day. Then

$$N = 2$$

$$N_{o} = 1$$

$$t-t_{o} = 1$$

and

$$k = 0.693 = ln 2$$
 (12)

$$k_{10} = 0.301 = log_{10} 2, k = 2.3026 k_{10}$$
 (13)

$$k_2 = 1.0 = \log_2 2, k = 0.6931 k_2$$
 (14)

Or, let the algal population quadruple in one day. Then

$$N = 4$$

$$N_{O} = 1$$

$$t-t_{O} = 1$$

and

$$k = 1.386 = ln 4$$
 (15)

$$k_{10} = 0.602 = log_{10} 4, k = 2.3026 k_{10}$$
 (16)

$$k_2 = 2.0 = \log_2 4$$
,  $k = 0.6931 k_2$  (17)

Similarily, let the algal population halve in one day. Then

$$N = 0.5$$

$$N_{0} = 1$$

$$t-t_{0} = 1$$

and let

$$k = -0.693$$
 (18)

$$k_{10} = -0.301, k = 2.3026 k_{10}$$
 (19)

$$k_2 = -1.0, k = 0.6931 k_2$$
 (20)

Thus, the relation between the various growth rates is given by

$$k = 2.3026 k_{10}$$
 (21)

$$k = 0.6931 k_2$$
 (22)

The composite gross production rate for this compartment should also represent a weighted contribution for the dominant species, or the dominant functional groups, to be simulated by this compartment.

29. Literature values for TPMAX are given in Table 5.

Table 5

Gross production rates of phytoplankton (1/day)

| SPECIES                    | TPMAX | TEMP °C | REFERENCE                              |
|----------------------------|-------|---------|--|
| DIATOMS                    |       |         |  |
| Asterionella formosa       | 0.81  | 20      | Holm and Armstrong 1981                |
| Asterionella formosa       | 0.69  | 10      | Hutchinson 1957                        |
| Asterionella formosa       | 1.38  | 20      | Hutchinson 1957                        |
| Asterionella formosa       | 1.66  | 25      | Hutchinson 1957                        |
| Asterionella formosa       | 1.71  | 20      | Fogg 1969                              |
| Asterionella formosa       | 0.28  | 4       | Taĺĺing 1955                           |
| Asterionella formosa       | 0.69  | 10      | Talling 1955                           |
| Asterionella formosa       | 1.38  | 20      | Talling 1955                           |
| Asterionella formosa       | 2.2   | 20      | Hoogenhout and Amesz 1965              |
| Asterionella formosa       | 1.9   | 18.5    | Hoogenhout and Amesz 1965              |
| Asterionella japonica      | 1.19  | 22      | Fogg 1969                              |
| Asterionella japonica      | 1.3   | 18      | Hoogenhout and Amesz 1965              |
| Asterionella japonica      | 1.7   | 25      | Hoogenhout and Amesz 1965              |
| Biddulphia sp.             | 1.5   | 11      | Castenholz 1964                        |
| Coscinodiscus sp.          | 0.55  | 18      | Fogg 1969                              |
| Cyclotella meneghiniana    | 0.34  | 16      | Hoogenhout and Amesz 1965              |
| Cyclotella nana            | 3.4   | 20      | Hoogenhout and Amesz 1965              |
| Detonula confervacea       | 0.62  | 2       | Smayda 1969                            |
| Detonula confervacea       | 1.4   | 10      | Hoogenhout and Amesz 1965              |
| Ditylum brightwellii       | 2.1   | 20      | Paasche 1968                           |
| Fragilaria sp.             | 0.85  | 20      | Rhee and Gotham 1981b                  |
| Fragilaria sp.             | 1.7   | 11      | Castenholz 1964                        |
| Melosira sp.               | 0.7   | 11      | Castenholz 1964                        |
| Navicula minima            | 1.4   | 25      | Hoogenhout and Amesz 1965              |
| Navicula pelliculosa       | 2.0   | 20      | Hoogenhout and Amesz 1965              |
| Nitzschia closterium       | 1.66  | 27      | Harvey 1937                            |
| Nitzschia palea            | 2.1   | 25      | Hoogenhout and Amesz 1965              |
| Nitzschia turgidula        | 2.5   | 20      | Paasche 1968                           |
| Phaeodactylum tricornutum  | 1.66  | 25      | Fogg 1969                              |
| Phaeodactylum tricornutum  | 2.7   | 19      | Hoogenhout and Amesz 1965              |
| Rhizosolenia fragillissima | 1.20  | 21      | Ignatiades & Smayda 1970               |
| Skeletonema costatum       | 1.26  | 18      | Fogg 1969                              |
| Skeletonema costatum       | 2.30  | 20      | Jorgensen 1968                         |
| Skeletonema costatum       | 1.52  | 20      | Steemann-Nielsen and<br>Jorgensen 1968 |
| Skeletonema costatum       | 1.23  | 20      | Jitts et al. 1964                      |
| Synedra sp.                | 1.2   | 11      | Castenholz 1964                        |
| Thalassiosira              |       |         | •                                      |
| norđenskioldii             | 0.77  | 13      | Jitts et al. 1964                      |
| natural diatom community   | 3.10  | 20      | Verđuin 1952                           |
| GREENS                     | 2 22  | 25      |  |
| Ankistrodesmus braunii     | 2.33  | 25      | Hoogenhout and Amesz 1965              |
| Chlamydomonas moewusii     |       | 4.2     | Hoogenhout and Amesz 1965              |
| Chlorella pyrenoidosa      | 2.22  | 28      | Shelef 1968                            |
| Chlorella ellipsoidea      | 3.6   | 25      | Hoogenhout and Amesz 1965              |
| Chlorella luteoviridis     | 0.56  | 22.4    | Hoogenhout and Amesz 1965              |
| Chlorella miniata          | 0.87  | 25      | Hoogenhout and Amesz 1965              |
| Chlorella pyrenoidosa      | 2.14  | 25      | Fogg 1969                              |

Table 5 (continued)

| SPECIES                                    | TPMAX | TEMP °C | REFERENCE                 |
|--|-------|---------|---------------------------|
| Chlorella pyrenoidosa                      | 1.95  | 25.5    | Sorokin and Myers 1953    |
| Chlorella pyrenoidosa                      | 9.00  | 39      | Castenholz 1969           |
| Chlorella pyrenoidosa                      | 9.2   | 39      | Hoogenhout and Amesz 1965 |
| Chlorella seccharophilia                   | 1.2   | 25      | Hoogenhout and Amesz 1965 |
| Chlorella variegata                        | 0.86  | 25      | Hoogenhout and Amesz 1965 |
| Chlorella vulgaris                         | 2.9   | 25      | Hoogenhout and Amesz 1965 |
| Chlorella vulgaris                         | 1.59  | 20      | Goldman and Graham 1981   |
| Dunaliella tertiolecta                     | 1.0   | 16      | Hoogenhout and Amesz 1965 |
| Dunaliella tertiolecta                     | 0.77  | 36      | Jitts et al. 1964         |
| Haematococcus pluvialis                    | 1.2   | 23      | Hoogenhout and Amesz 1965 |
| Nanochloris atomus                         | 1.0   | 20      | Hoogenhout and Amesz 1965 |
| Platymonas subcordiformia                  | 1.5   | 16      | Hoogenhout and Amesz 1965 |
| Scenedesmus sp.                            | 1.34  | 20      | Rhee and Gotham 1981b     |
| Scenedesmus costulatus                     | 2.0   | 24.5    | Hoogenhout and Amesz 1965 |
| Scenedesmus obliquus                       | 2.11  | 20      | Goldman and Graham 1981   |
| Scenedesmus obliquus                       | 2.2   | 25      | Hoogenhout and Amesz 1965 |
| Scenedesmus quadricauda                    | 4.1   | 25      | Hoogenhout and Amesz 1965 |
| Scenedesmus quadricauda                    | 2.29  | 27      | Goldman et al. 1972       |
| Selenastrum capricornutum                  | 2.45  | 27      | Goldman et al. 1972       |
| Selenastrum westii                         | 1.0   | 25      | Hoogenhout and Amesz 1965 |
| Stichococcus sp.                           | 0.70  | 20      | Hoogenhout and Amesz 1965 |
| GOLDEN-BROWN                               |       |         |                           |
| Botrydiopsis intercedens                   | 1.5   | 25      | Hoogenhout and Amesz 1965 |
| Bumilleriopsis brevis                      | 2.9   | 25      | Hoogenhout and Amesz 1965 |
| Cricosphaera carterae                      | 0.82  | 18      | Fogg 1969                 |
| Isochrysis galbana                         | 0.55  | 20      | Fogg 1969                 |
| Isochrysis galbana                         | 0.80  | 25      | Hoogenhout and Amesz 1965 |
| Monochrysis lutheri                        | 1,5   | 15      | Hoogenhout and Amesz 1965 |
| Monochrysis lutheri                        | 0.39  | 24      | Jitts et al. 1964         |
| Monodus subterraneus                       | 0.93  | 25      | Hoogenhout and Amesz 1965 |
| Monodus subterraneus                       | 0.39  | 30      | Fogg 1969                 |
| Tribonema aequale                          | 0.70  | 25      | Hoogenhout and Amesz 1965 |
| Tribonema minus                            | 1.00  | 25      | Hoogenhout and Amesz 1965 |
| Vischeria stellata                         | 0.70  | 25      | Hoogenhout and Amesz 1965 |
| Euglena gracilis                           | 2.2   | 25      | Hoogenhout and Amesz 1965 |
| Euglena gracilis                           | 0.00  | 36      | Marre 1962                |
| DINOFLAGGELATE                             |       |         |                           |
|  | 1.88  | 18      | Fogg 1969                 |
| Amphidinium carteri<br>Amphidinium carteri | 0.32  | 32      | Jitts et al. 1964         |
|  | 0.32  | 20      | Fogg 1969                 |
| Ceratium tripos<br>Gonyaulax polyedra      | 2.1   | 21.5    | Hoogenhout and Amesz 1965 |
| Gymnodinium splendens                      | 0.92  | 20      | Hoogenhout and Amesz 1965 |
| Peridinium sp.                             | 0.92  | 18      | Hoogenhout and Amesz 1965 |
| Prorocentrium gracile                      | 0.83  | 18      | Hoogenhout and Amesz 1965 |
| Prorocentrium micans                       | 0.71  | 25      | Hoogenhout and Amesz 1965 |
| Prorocentrium micans                       | 0.30  | 20      | Fogg 1969                 |
| 2 20 20001102 2 am maouito                 | 0.50  |         |                           |

Table 5 (concluded)

| SPECIES                    | TPMAX | TEMP °C    | REFERENCE                               |
|----------------------------|-------|------------|---|
| BLUEGREENS                 |       |            | <u>-</u>                                |
| Agmenellum quadriplaticum  | 8.0   | 39         | Hoogenhout and Amesz 1965               |
| Anabaena cylindrica        | 0.96  | 25         | Hoogenhout and Amesz 1965               |
| Anabaena variabilis        | 3.9   | 34.5       | Hoogenhout and Amesz 1965               |
| Anacystis nidulans         | 2.9   | 25         | Hoogenhout and Amesz 1965               |
| Anacystis nidulans         | 8.28  | 38         | Marre 1962                              |
| Anacystis nidulans         | 11.00 | 40         | Castenholz 1969                         |
| Chloropseudomonas          |       |            |   |
| ethylicum                  | 3.3   | 30         | Hoogenhout and Amesz 1965               |
| Cyanidium caldarium        | 2.4   | 40         | Hoogenhout and Amesz 1965               |
| Cylindrospermum sphaerica  | 0.17  | 25         | Hoogenhout and Amesz 1965               |
| Gloeotrichia echinulata    | 0.20  | 26.5       | Hoogenhout and Amesz 1965               |
| Microcystis aeruginosa     | 0.25  | 20         | Holm and Armstrong 1981                 |
| Microcystis aeruginosa     | 1.6   | 23         | Hoogenhout and Amesz 1965               |
| Microcystis luminmosis     | 1.50  | 40         | Castenholz 1969                         |
| Nostoc muscorum            | 2.9   | 32.5       | Hoogenhout and Amesz 1965               |
| Oscillatoria princips      | 0.50  | 40         | Castenholz 1969                         |
| Oscillatoria subbrevis     | 5.52  | 38         | Marre 1962                              |
| Oscillatoria terebriformis | 3.36  | 40         | Castenholz 1969                         |
| Oscillatoria rubescens     | 5.04  | 3 <b>0</b> | Zimmerman 1969                          |
| Rhodopseudomonas           |       |            |   |
| sphaeroides                | 10.8  | 34         | Hoogenhout and Amesz 1965               |
| Rhodospirllum rubrum       | 4.85  | 25         | Hoogenhout and Amesz 1965               |
| Schizothrix calcicola      | 3.4   | 30         | Hoogenhout and Amesz 1965               |
| Synechococcus lividus      | 4.98  | 40         | Castenholz 1969                         |
| Synechococcus sp.          | 8.0   | 37         | Hoogenhout and Amesz 1965               |
| Tolypothrix tenuis         | 4.0   | 38         | Hoogenhout and Amesz 1965               |
| Leptocylindrus danicus     | 0.67- | 10-        |   |
|                            | 2.0   | 20         | Verity 1981                             |
| Anabaena variabilis        | 0.07- | 10-        | • · · · · · · · · · · · · · · · · · · · |
|                            | 2.0   | 35         | Collins and Boylen 1982a                |

#### TSETL

- 30. TSETL is the phytoplankton settling rate (m/day). Mechanisms of suspension can influence the settling or sinking rate of algae. Morphological mechanisms include cell size, colony formation, cyclomorphosis, protuberances, and flagella. Physiological mechanisms include fat accumulation; regulation of ionic composition of cell sap; and the response of an organism to light, photoperiod, and nutrient concentration. Physical mechanisms include water viscosity and the role of water movements.
- 31. Two methods used to measure sinking rates experimentally are (a) the settling chamber method with or without the use of a microscope, and (b) the photometric tech-In the settling chamber, the descent time is determined (a) by following with a microscope or, in the case of large particles, with the naked eye, the cell trajectory between two marks at a known distance apart; (b) by measuring the time a cell takes to fall to the bottom of a settling chamber of known height placed on the stage of an inverted scope; or (c) using a 1-mm-deep Sedgwick Rafter counting chamber with a compound microscope. mation of relative sinking rate has been obtained by placing a well-mixed suspension of phytoplankton into a graduated cylinder and determining the concentration in various layers after a given time.
- 32. Photometric determination of sinking rate measures changes in optical density of a phytoplankton suspension measured at 750 nm after introducing the phytoplankton suspension into a cuvette.
- 33. These techniques are influenced by the "wall-effect," that is, the effect of the settling chamber wall and convection current on the sinking velocity. To provide adequate fall for attainment of terminal velocity and to

minimize overcrowding, the selection of chamber size is important.

- 34. The sinking rates of natural populations have also been determined by comparing changes in population density with depth and calculating a mean rate of descent. However, determination of sinking rate in situ is complicated by water movements and losses due to grazing. Mathematical expressions may also be used to determine sinking rates (Riley et al. 1949).
- 35. The application of experimentally determined sinking rates to natural populations or ecosystem models must be qualified and used with caution. In lakes and reservoirs, vertical gradients of light, temperature, and nutrient concentration contrast with the constancy of the settling chamber and photometer cuvette environments in sinking experiments. The influence of light and nutrients on sinking rates together with the turbulent motion of the natural environment suggest that in vitro sinking results may not be particularly representative of natural populations. Values for settling rates are given in Table 6.

Table 6
Phytoplankton settling rates (m/day)

| SPECIES                                    | TSETL                                   | REFERENCE              |
|--|---|------------------------|
| DIATOMS                                    |   | <del></del>            |
| EXPERIMENTAL STUDIES                       |   |                        |
| Asterionella formosa                       | 0.26-0.76                               | Smayda 1974            |
| Asterionella formosa                       | 0.4                                     | Margalef 1961          |
| Bacteriastrum hyalinum                     | 0.39-1.27                               | Smayda & Boleyn 1966   |
| Chaetoceros didymus                        | 0.85                                    | Eppley et al. 1967b    |
| Chaetoceros didymas<br>Chaetoceros lauderi | 0.46-1.54                               | Smayda & Boleyn 1966   |
| Chaetoceros lauderi                        | 0.46-1.54                               | Smayda & Boleyn 1966   |
| Chaetoceros spp.                           | 0.25                                    | Margalef 1961          |
| Chaetoceros spp.                           | 5.0                                     | Sverdrup et al. 1942   |
| Chaetoceros spp.                           | 4.0                                     | Allen 1932             |
| Coscinodiscus wailesii                     | 7.0-30.2                                | Eppley et al. 1967b    |
| Coscinodiscus sp.                          | 1.95-6.83                               | Eppley et al. 1967b    |
| Coscinodiscus sp.                          | 14.7                                    | Eppley et al. 1967b    |
| Cyclotella meneghiniana                    | 0.08-0.24                               | Titman and Kilham 1976 |
| Cyclotella mana                            | 0.16-0.76                               | Eppley et al. 1967b    |
| Ditylum brightwellii                       | 0.60-3.09                               | Eppley et al. 1967b    |
| Ditylum brightwellii                       | 2.                                      | Eppley et al. 1967b    |
| Ditylum brightwellii                       | 5.8-8.6                                 | Gross & Zeuthen 1948   |
| Fragilaria crotonensis                     | 0.27                                    | Burns and Ross 1980    |
| Leptocylindrus danicus                     | 0.08-0.42                               | Margalef 1961          |
| Melosira agassizii                         | 0.67-1.87                               | Titman and Kilham 1976 |
| Nitzschia closterium                       | 0.52                                    | Margalef 1961          |
| Nitzschia seriata                          | 4.0                                     | Allen 1932             |
| Nitzschia seriata                          | 0.35-0.50                               | Smayda & Boleyn 1965   |
| Phaeodactylum tricornutum                  | 0.05-0.06                               | Riley 1943             |
| Phaeodactylum tricornutum                  | 0.02-0.04                               | Riley 1943             |
| Rhizosolenia hebetata                      | , |                        |
| f. semispina                               | 0.22                                    | Eppley et al. 1967b    |
| Rhizosolenia setigera                      | 0.11-2.23                               | Smayda & Boleyn 1966   |
| Rhizosolenia setigera                      | 0.10-6.30                               | Smayda & Boleyn 1966   |
| Rhizosolenia stolterfothii                 | 1.0-1.9                                 | Eppley et al. 1967b    |
| Rhizosolenia spp.                          | 0-0.72                                  | Margalef 1961          |
| Skeletonema costatum                       | 0.30-1.35                               | Smayda & Boleyn 1966   |
| Stephanopyxis turris                       | 1.1                                     | Eppley et al. 1967b    |
| Stephanopyxis turris                       | 2.1                                     | Eppley et al. 1967b    |
| Thalassionema nitzschiodes                 | 0.35-0.78                               | Smayda (unpubl.)       |
| Thalassiosira fluviatilis                  | 0.60-1.10                               | Eppley et al. 1967b    |
| Thalassiosira cf. nana                     | 0.10-0.28                               | Smayda & Boleyn 1965   |
| Thalassiosira rotula                       | 1.15                                    | Eppley et al. 1967b    |
| Thalassiosira rotula                       | 0.39-2.10                               | Smayda & Boleyn 1965   |
| Thalassiosira spp.                         | 0-0.16                                  | Margalef 1961          |
| THEORETICAL                                |   | - 1./1 10 <i>6</i> 1   |
| Diatoms                                    | 0.3                                     | Bramlette 1961         |

Table 6 (concluded)

| SPECIES                   | TSETL       | REFERENCE           |
|---------------------------|-------------|---------------------|
| DINOFLAGELLATES           | <del></del> | <del></del>         |
| EXPERIMENTAL STUDIES      |             |                     |
| Gonyaulax polyedra        | 2.8-6.0     | Eppley et al. 1967b |
| COCCOLITHOPHORIDS         |             |                     |
| EXPERIMENTAL STUDIES      |             |                     |
| Coccolithus huxleyi       | 0.28        | Eppley et al. 1967b |
| Coccolithus huxleyi       | 1.20        | Eppley et al. 1967b |
| Cricosphaera carterae     | 1.70        | Eppley et al. 1967b |
| Cricosphaera elongata     | 0.25        | Eppley et al. 1967b |
| Cyclococcolithus fracilis | 13.2        | Bernard 1963        |
| Cyclococcolithus fragilis | 13.6        | Bernard 1963        |
| Cyclococcolithus fragilis | 10.3        | Bernard 1963        |
| THEORETICAL               |             |                     |
| Coccoliths                | 1.5         | Bramlette 1961      |
| MICROFLAGELLATES          |             |                     |
| EXPERIMENTAL STUDIES      |             |                     |
| Cryptomonas erosa         | 0.31        | Burns and Rosa 1980 |
| Cryptomonas marsonii      | 0.32        | Burns and Rosa 1980 |
| Rhodomonas minuta         | 0.07        | Burns and Rosa 1980 |
| Dunaliella tertiolecta    | 0.18        | Eppley et al. 1967b |
| Monochrysis lutheri       | 0.39        | Eppley et al. 1967b |
| Monochrysis lutheri       | 0.39        | Apstein 1910        |
| GREENS EXPERIMENTAL       |             | •                   |
| Closterium parvulum       | 0.18        | Burns and Rosa 1980 |
| Dunaliella tertiolecta    | 0.18        | Eppley et al. 1967b |
| Lagerhaemia quadriseta    | 0.08        | Burns and Rosa 1980 |
| Scenedesmus acutiformis   | 0.10        | Burns and Rosa 1980 |
| Selenastrum minutum       | 0.15        | Burns and Rosa 1980 |
| BLUEGREENS EXPERIMENTAL   |             | •                   |
| Anabaena spiroides        | 0.10        | Burns and Rosa 1980 |
| Gomphosphaeria lacustris  | 0.11        | Burns and Rosa 1980 |
|                           |             |                     |

### PS2P04

- 36. PS2P04 is the phosphorus half-saturation coefficient (HSC) (mg/L). In practical terms, the HSC of a nutrient approximately marks the upper nutrient concentration at which growth ceases to be proportional to that nutrient. The modeled uptake of phosphorus by algae follows Monod kinetics. The value of the HSC can be calculated for the hyperbola using the Monod equation. PS2P04 is defined as the concentration of phosphorus at which the rate of uptake is one-half the maximum.
- 37. Half-saturation coefficients generally increase with nutrient concentrations (Hendrey and Welch 1973, Carpenter and Guillard 1971, and Toetz et al. 1973). This fact reflects both the change in species composition of the phytoplankton assemblage and the adaptation of the plankton to higher nutrient levels. A reservoir characterized by low nutrient concentrations is generally also characterized by low half-saturation coefficients. Phosphorus is commonly the nutrient that limits the growth of algae in lakes and reservoirs.
- 38. The procedure of measuring a phosphorus half-saturation coefficient involves the measurement of the net rate of loss of dissolved orthophosphate from the medium in which the experimental population is suspended.
- 39. Units of measurement must be expressed in terms of the chemical element and not the compound; i.e., the half-saturation constant for phosphorus should be specified as mg/L of phosphorus and not mg/L of orthophosphate. Micromoles per liter or microgram-atom values may be converted by multiplying by the molecular weight of the element times 10<sup>-3</sup>. Values for the HSC are given in Table 7.

Table 7
Phytoplankton half-saturation coefficients for P limitation (mg/L)

| SPECIES   | PS2PO4  | REFERENCE   |
|---|---|---|
| Asterionella formosa Asterionella japonica Biddulphia sinensis Cerataulina bergonii Chaetoceros curvisetus Chaetoceros socialis Chlorella pyrenoidosa Cyclotella nana Cyclotella nana Dinobryon cylindricum Dinobryon sociale | 0.002<br>0.014<br>0.016<br>0.003<br>0.074105<br>0.001<br>0.38475<br>0.055<br>0.001<br>0.076 | Holm and Armstrong 1981 Thomas and Dodson 1968 Quasim et al. 1973 Finenko and Krupatikina 1974 Finenko and Krupatikina 1974 Finenko and Krupatikina 1974 Jeanjean 1969 Fuhs et al. 1972 Fogg 1973 Lehman (unpubl. data) |
| var. americanum Euglena gracilis Freshwater phytoplankton Microcystis aeruginosa Nitzschia actinastreoides Pediastrum duplex Pithophora oedogonia Scenedesmus obliquus Scenedesmus sp. Thalassiosira fluviatilis              | 0.047<br>1.52<br>0.02075<br>0.006<br>0.095<br>0.105<br>0.098<br>0.002<br>0.00205<br>0.163   | Lehman (unpubl. data) Blum 1966 Halmann and Stiller 1974 Holm and Armstrong 1981 von Muller 1972 Lehman (unpubl. data) Spencer and Lembi 1981 Fogg 1973 Rhee 1973 Fogg 1973   |

- 40. PS2N is the nitrogen (N) half-saturation coefficient (mg/L). Uptake rates of nitrate (NO3) or ammonium (NH4) by algae give hyperbolas when graphed against NO3 or NH4 concentration in the environment. Half-saturation coefficients (i.e., the concentration of N at which the rate of production is one-half the maximum) can be calculated for the hyperbolas using the Monod equation. This constant reflects the relative ability of phytoplankton to use low levels of nitrogen.
- 41. The role of N as a growth-limiting factor has been relatively neglected when compared with phosphorus, presumably because the latter is the growth-limiting factor in most natural fresh waters. However, it has been found that nitrogen becomes the limiting nutrient where phosphorus is abundant because of its release from geological deposits or from external loadings.
- There are several methods for measuring half-42. saturation constants for N limitation. The chemostat method requires the measurement of the remaining nitrogen concentration at a number of fixed dilution rates (i.e., growth rates) in nitrogen-limited chemostat cultures. Culture media are prepared with nitrate or ammonium as the nitrogen source, with one-fifth or less than the usual amount of NO3 or NH4 added to the culture media to ensure that during growth, nitrogen will be depleted before other nutrients. A second, less desirable, method is to use nitrogen-starved cells as an innoculum for cultures containing known concentrations of nitrogen and then (a) measure the concentration of nitrogen in the extracellular fluid at some later time to determine the rate of nitrogen uptake and (b) measure the increasing cell concentration to determine growth kinetics. The problems associated

with this method are that the organisms are poorly adapted to their subsequent growth environment, so growth can occur only after uptake of a substantial amount of nitrogen.

- 43. Some trends can be seen in the data for half-saturation coefficients: (a) organisms with a high HSC for nitrate usually have a high HSC for ammonium uptake as well, (b) large-celled species tend to show higher HSC's, (c) fast-growing species tend to have lower HSC's than slow growers.
- 44. The nitrogen HSC as used in CE-QUAL-Rl should reflect the uptake of both NO3 and NH4. Both compounds are taken up for use in production in proportion to their concentration in the layer.
- 45. A factor that will lead to selection for a particular functional group or species is the availability of combined nitrogen. In situations where the level of combined nitrogen is relatively low compared with other essential elements like phosphorus, those bluegreen species that can fix nitrogen will be at a selective advantage. Nitrogen fixation is not explicitly included in the model formulation for phytoplankton; however, if bluegreen algae are an important component in one of the compartments, the nitrogen half-saturation coefficient may have to be reduced to a low value to reflect nitrogen fixation. Values for the HSC for nitrogen are given in Table 8.

Table 8

Phytoplankton half-saturation coefficients for N limitation (mg/L)

|                            |          | · · · · · · · · · · · · · · · · · · · |                           |
|----------------------------|----------|---------------------------------------|---------------------------|
|                            | _        | N                                     | _                         |
| SPECIES                    | PS2N     | SOURCE                                | REFERENCE                 |
| DIATOMS                    |          |                                       |                           |
| Biddulphia aurita          | 0.056197 | NO3                                   | Underhill 1977            |
| Chaetoceros gracilis       | 0.012    | NO3                                   | Eppley et al. 1969        |
| Chaetoceros gracilis       | 0.007    | NO4                                   | Eppley et al. 1969        |
| Coscinodiscus lineatus     | 0.161    | NO3                                   | Eppley et al. 1969        |
| Coscinodiscus lineatus     | 0.036    | NH4                                   | Eppley et al. 1969        |
| Cyclotella nana            | 0.025117 | NO3                                   | Carpenter & Guillard 1971 |
| Cyclotella nana            | 0.111    |                                       | MacIssac and Dugdale 1969 |
| Cyclotella nana            | 0.027    |                                       | Caperon and Meyer 1972    |
| Cyclotella nana            | 0.031    |                                       | Eppley et al. 1969        |
| Cyclotella nana            | 0.007    | NH 4                                  | Eppley et al. 1969        |
| Ditylum brightwellii       | 0.037    | NO3                                   | Eppley et al. 1969        |
| Ditylum brightwellii       | 0.020    | NH4                                   | Eppley et al. 1969        |
| Dunaliella teriolecta      | 0.013    | NO3                                   | Caperon and Meyer 1972    |
| Dunaliella teriolecta      | 0.003    | NH 4                                  | Caperon and Meyer 1972    |
| Dunaliella teriolecta      | 0.087    | NO3                                   | Eppley et al. 1969        |
| Fragilaria pinnata         | 0.037100 | NO3                                   | Carpenter & Guillard 1971 |
| Leptocylindrous danicus    | 0.078    | NO3                                   | Eppley et al. 1969        |
| Leptocylindrous danicus    | 0.013    | NH4                                   | Eppley et al. 1969        |
| Navicula pelliculosa       | 0.923    | NO3                                   | Wallen and Cartier 1975   |
| Phaeodactylum tricornutum  |          | NO3                                   | Ketchum 1939              |
| Rhizosolenia robusta       | 0.186    | NO3                                   | Eppley et al. 1969        |
| Rhizosolenia robusta       | 0.135    | NH 4                                  | Eppley et al. 1969        |
| Rhizosolenia               |          |                                       |                           |
| stolterfothii              | 0.105    | NO3                                   | Eppley et al. 1969        |
| Rhizosolenia               | :        |                                       |                           |
| stolterfothii              | 0.009    | NH4                                   | Eppley et al. 1969        |
| Skeletonema costatum       | 0.027    | NO3                                   | Eppley et al. 1969        |
| Skeletonema costatum       | 0.014    | NH 4                                  | Eppley et al. 1969        |
|                            |          |                                       |                           |
| BLUEGREENS                 |          |                                       |                           |
| Anabaena cylindrica        | 4.34     | NO3                                   | Hattori 1962              |
| Anabaena cylindrica        | 2.48     | NO2                                   | Hattori 1962              |
| Asterionella formosa       | 0.074093 | иоз                                   | Eppley and Thomas 1969    |
| Asterionella formosa       | 0.062    | NH 4                                  | Eppley and Thomas 1969    |
| Microcystis aeruginosa     | 0.56207  | NH4                                   | Kappers 1980              |
| Oscillatoria agarthii      | 0.22     | иоз                                   | van Liere et al. 1975     |
| MICROFLAGELLATES           |          | :                                     |                           |
| Bellochia sp.              | 0.001016 | NO3                                   | Carpenter & Guillard 1971 |
| Monochrysis lutheri        | 0.001010 | NO3                                   | Caperon and Meyer 1972    |
| Monochrysis lutheri        | 0.052    | NH4                                   | Caperon and Meyer 1972    |
| Monochrysis lutheri        | 0.032    | NO3                                   | Eppley et al. 1969        |
| Monochrysis lutheri        | 0.037    | NH 4                                  | Eppley et al. 1969        |
| MONOCHEASTS TARRETT        | 0.007    | FAST_Z                                | Thatel of ar. 1202        |
| COCCOLITHOPHORIDS          |          |                                       |                           |
| Coccolithus huxleyi        | 0.006    | NO3                                   | Eppley et al. 1969        |
| Coccolithus huxleyi        | 0.002    | NH4                                   | Eppley et al. 1969        |
| Coccochloris stagnina      | 0.019    | NO3                                   | Caperon and Meyer 1972    |
| 이 생기 말이네가 무릎이 맛이 뭐라는 생각이다. |          | 1.0                                   |                           |

(continued)

Table 8 (concluded)

| SPECIES   | PS2N   | n<br>SOURCE                            | REFERENCE   |
|---|--|--|---|
| GREENS<br>Chlorella pyrendoidosa<br>Chlorella pyrendoidosa<br>Pithophora oedogonia  | 0.006014<br>1.15<br>1.236                          | NO2<br>NO3                             | Pickett 1975<br>Knudsen 1965<br>Spencer and Lembi 1981  |
| DINOFLAGELLATES Gonyaulax polyedra Gonyaulax polyedra Gymnodinium splendens Gymnodinium splendens Gymnodinium wailesii Gymnodinium wailesii | 0.589<br>0.099<br>0.235<br>0.019<br>0.223<br>0.088 | NO3<br>NH4<br>NO3<br>NH4<br>NO3<br>NH4 | Eppley et al. 1969 |
| CHRYSOPHYTES<br>Isochrysis galbana  | 0.006  | NO3                                    | Eppley et al. 1969  |

#### PS2C02

- 46. PS2CO2 is the half-saturation coefficient for carbon dioxide (mg/L). The coefficient is used in the Monod equation to determine the rate factor for CO2 limitation. PS2CO2 is defined as the concentration of CO2 at which the rate of production is one-half the maximum. In practical terms, the HSC approximately marks the upper nutrient concentration at which growth ceases to be proportional to that nutrient.
- There is a diversity of opinions as to whether 47. inorganic carbon (C) limits photosynthesis in phytoplankton. Goldman et al. (1974) have argued that inorganic carbon almost never limits growth in natural algal populations. In contrast, King (1970) has shown that CO2 availability limits the growth of aquatic populations. Johnson et al. (1970) demonstrated CO2 limitation in lakes contaminated by acid mine wastes, and Schindler and Fee (1973) demonstrated C limitation in a lake during the summer when nitrogen and phosphorus were available. Carbon dioxide limitation is clearly pH dependent. For example, the HSC for carbon dioxide given in Table 9 for Scenedesmus capricornutum increases with increasing pH. This is related to the effect of pH on the relative proportions of the inorganic carbon species of carbon dioxide, bicarbonate ion, and carbonate ion in solution. Half-saturation coefficient values for carbon dioxide are given in Table 9.

Table 9

Phytoplankton half-saturation coefficients for CO2 limitation (mg/L)

| SPECIES  | PS2CO2  | ph RANGE                                     | REFERENCE  |
|--|---|--|--|
| Chlorella vulgaris Chlorella emersonii Mixed bluegreen algae Mixed bluegreen algae Mixed bluegreen algae Scenedesmus quadricauda Scenedesmus quadricauda Scenedesmus quadricauda | 0.20<br>0.068411<br>0.088<br>0.031<br>0.057<br>0.14<br>0.36<br>0.5471 | 7.1-7.2<br>7.1-7.2<br>7.25-7.39<br>7.44-7.61 | Goldman and Graham 1981<br>Beardall and Raven 1981<br>Golterman 1975<br>Forester 1971<br>Shamieh 1968<br>Goldman et al. 1974<br>Goldman et al. 1974<br>Goldman et al. 1974 |
| Scenedesmus<br>capricornutum<br>Scenedesmus  | 0.4041  | 7.05-7.2                                     | Goldman et al. 1974  |
| capricornutum Scenedesmus capricornutum Scenedesmus obliquus   | 0.63-1.0<br>1.2-1.5<br>0.16   | 7.25-7.39<br>7.43-7.59<br>7.1-7.2            | Goldman et al. 1974 Goldman et al. 1974 Goldman and Graham 1981  |

## PS2L

- 48. PS2L is the light half-saturation coefficient expressed as  $kcal/m^2/hr$ . It is the light intensity at which the rate of production is at one-half the maximum rate.
- 49. The shape of the curve relating light and production has been studied extensively. It is generally known that (a) at lower light intensities, production proceeds linearly with increasing light intensity and (b) as intensity is increased further, the production rate tends towards a maximum value. The simplest representation of this response is the Monod function.
- 50. It has been shown that the photosynthetic rate of certain algal species is inhibited at high light intensities. This phenomenon cannot be simulated by the Monod function used in CE-QUAL-R1. Other formulations have been developed to represent this effect (Steele 1962). Photoinhibition at high light intensities may be more important in oligotrophic waters than in eutrophic waters.
- 51. The value of this parameter can be obtained by running a set of experiments to determine the production rate at various light intensities ranging from light-limiting to light-saturating conditions. The value can be determined for net photosynthetic rate by measuring 14 carbon, fixed or oxygen evolved, at different light levels. The light half-saturation constant for growth rate can be determined by measuring growth rate (i.e., by measuring either dry weight, cell volume, chlorophyll concentration, or optical density) at various light intensities. Values for the HSC for light intensity are given in Table 10.

Table 10 Phytoplankton half-saturation coefficients for light limitation  $\frac{(kcal/m^2/hr)}{}$ 

| SPECIES                 | PS2L      | PROCESS    | REFERENCE                 |
|-------------------------|-----------|------------|---------------------------|
| Amphidinium carteri     | 5.75      |            | Dunstan 1973              |
| Amphiprora sp.          | 6.42      | growth     | Admiraal 1977             |
| Chlorella pyrenoidosa   | 12.7-38.0 | photosyn   | Myers and Graham 1961     |
| Chlorophyte             | 1.2-4.2   |            | Bates 1976                |
| Chroomonas salina       | 6.25      | growth     | Hobson 1974               |
| Coccolithus huxleyi     | 1.2       | _          | Parsons & Takahashi 1973  |
| Coccolithus huxleyi     | 5.75      |            | Dunstan 1973              |
| Cryptomonas ovata       | 16.0      | growth     | Cloern 1977               |
| Cyclotella nana         | 5.15      | growth     | Dunstan 1973              |
| Ditylum brightwelli     | 5.4       |            | Bates 1976                |
| Fragilaria sp.          | 9.4       | growth     | Rhee and Gotham 1981b     |
| Gonyaulax polyedra      | 15.4-18.9 | growth     | Prezelin and Sweeney 1977 |
| Gonyaulax polyedra      | 15.4-19.1 | photosyn   | Prezelin and Sweeney 1977 |
| Isochrysis galbana      | 6.18      | _          | Dunstan 1973              |
| Isochrysis sp.          | 5.0       | growth     | Hobson 1974               |
| Mixed population        | 16.0      | growth     | Gargas 1975               |
| Navicula arenaria       | 6.42      | growth     | Admiraal 1977             |
| Nitzschia dissipata     | 6.64      | growth     | Admiraal 1977             |
| Oscillatoria agardhii   | 0.8       | growth     | van Lierre et al. 1978    |
| Phaeodactylum           |           | -          |                           |
| tricornutum             | 51.0-71.4 | photosyn   | Li and Morris 1982        |
| Prorocentrum micans     | 5.66      | _ <u>-</u> | Dunstan 1973              |
| Scenedesmus protuberans | 2.57      | growth     | van Lierre et al. 1978    |
| Scenedesmus sp.         | 6.0       | growth     | Rhee and Gotham 1981b     |
| Scenedesmus sp.         | 6.8       | photosyn   | Rhee and Gotham 1981b     |
| Skeletonema costatum    | 0.18-4.2  | _          | Bates 1976                |
| Thalassiosira           |           |            |                           |
| fluvatilis              | 6.25      | growth     | Hobson 1974               |
| Thalassiosira           |           |            |                           |
| nordenskioldii          | 12.0      | growth     | Durbin 1974               |

## ALGT1, ALGT2, ALGT3, ALGT4

- 52. All temperature coefficients are in degrees Celsius.
  - <u>a.</u> ALGTl is the lower temperature bound at which phytoplankton metabolism continues.
  - b. ALGT2 is the lowest temperature at which processes are occurring near the maximum rate.
  - c. ALGT3 is the upper temperature at which processes are occurring at the maximum rate.
  - d. ALGT4 is the upper lethal temperature.
    Biological temperature curves are generally asymmetrical, with the maximum rates occurring nearer the upper lethal temperatures than the lower temperatures.
- 53. Temperature acclimation. The temperature coefficients for algal production are dependent upon the acclimation temperature and the length of time the alga has been exposed to this temperature (Collins and Boylen 1982b) since algae are exposed to seasonal temperature changes in various regions of the United States. For example, algae growing in a northern reservoir will have a lower optimum temperature (ALGT2 and ALGT3) than algae growing in a southern reservoir because the northern algae have become acclimated to different climatic regimes. The lower and upper temperature boundaries (ALGT1 and ALGT4) will also be affected by acclimation and will differ substantially among different functional groups of algae.
- 54. Unfortunately, there is no set rule to determine these coefficients based upon site-specific temperature regimes. One can estimate these values for a given species or functional group based upon reported experimental conditions or in situ study conditions. Several investigators have determined these values based upon studies where several physical factors such as light intensity,

temperature, and day length have been varied simultaneously. Often the algae were preconditioned at a specific combination of these factors, which may help in parameter estimation for a particular site. Values for the temperature coefficients are given in Table 11.

Table 11
Temperature coefficients for phytoplankton (°C)

| SPECIES                         | ALGT1 | ALGT2 | ALGT3 | ALGT4 | REFERENCE                              |
|---------------------------------|-------|-------|-------|-------|--|
| Amphidinium carteri             | 18    | 24    |       | 35    | Jitts et al. 1964                      |
| Anacystis nidulans              |       | 38    | 40    |       | Castenholz 1969                        |
| Asterionella formosa            |       | 25    | 25    |       | Rhee and Gotham 1981a                  |
| Asterionella formosa            |       | 25    | 29    |       | Hutchinson 1967                        |
| Asterionella formosa            | 4     | 20    | 25    |       | Talling 1955                           |
| Chlorella pyrenoidosa           | 1     | 28    | 38    | 40    | Clendenning et al. 1956                |
| Chlorella pyrenoidosa           | 7     | 38    | 40    | 42    | Sorokin & Krauss 1962                  |
| Chlorella sp.                   |       | 20    | 25    |       | Tamiya et al. 1965                     |
| Detonula confervacea            | 0     | 10    | 12    | 16    | Guillard & Ryther 1962                 |
| Detonula confervacea            | 1     | 10    | 13    | 15    | Smayda 1969                            |
| Ditylum brightwellii            | 5     | 23    | 26    | 30    | Paasche 1968                           |
| Dunaliella teriolecta           | 8     | 31    | 33    | 36    | Eppley and Sloan 1966                  |
| Dunaliella teriolecta           | 12    | 26    | 28    | 36    | Jitts et al. 1964                      |
| Microcystis aeruginosa          |       | 38    | 40    |       | Castenholz 1969                        |
| Monochrysis lutheri             | 9     | 19    | 22    |       | Jitts et al. 1964                      |
| Nitzschia closterium            |       | 27    | 30    |       | Harvey 1955                            |
| Nostoc muscorum<br>Oscillatoria | 1     | 31    | 33    | 36    | Clendenning et al. 1956                |
| terebriformis                   |       | 38    | 40    |       | Castenholz 1969                        |
| Phaeodactylum                   |       |       |       |       |  |
| tricornutum                     | 0     | 20    | 21    | 30    | Li and Morris 1982                     |
| Rhizosolenia                    |       |       |       |       |  |
| fragillissima                   | 7     | 21    |       |       | Ignatiades and Smayda<br>1970          |
| Scenedesmus sp.                 |       | 19    | 20    | 21    | Rhee and Gotham 1981a                  |
| Skeletonema costatum            | 1     | 20    | ***   |       | Jorgensen 1968                         |
| Skeletonema costatum            | 2     | 20    |       |       | Steemann-Nielsen and<br>Jorgensen 1968 |
| Thalassiosira                   |       |       |       |       | -                                      |
| nordenskioldii                  | 4     | 13    | 14    | 16    | Jitts et al. 1964                      |

# Zooplankton

#### TZMAX

- 55. TZMAX is the maximum ingestion rate for zooplankton (1/day). The zooplankton compartment includes the groups Cladocera, Copepoda, and Rotatoria which are classified as either herbivores or as carnivores.
- 56. Two types of feeding behavior exist: filter feeding and grasping feeding. Daphnia and some copepods are filter feeders. They collect particulate matter, including algae and detritus, by sieving lake water through the fine meshes of their filtering apparatus (Jorgensen 1975). Algae are swept into the feeding appendages to the mouth region where they are ingested as boluses containing many cells. Filter-feeding zooplankton make up the greater proportion of the zooplankton community and have been studied in greater detail.
- 57. The filtering rate per animal decreases as food concentration increases; above a critical concentration of food, the feeding rate is independent of food concentration.
- 58. Factors that influence food consumption by filter-feeding zooplankton include (a) animal density, size, sex, reproductive state, nutritional or physiological state as well as (b) the type, quality, concentration, and particle size of food. Other factors include water quality and temperature.
- 59. A second type of feeding behavior, raptorial or grasping feeding, is exhibited by most copepods and some cladocerans. They pursue prey and grasp large particles, including algae and detritus. Apparently, some copepods can switch feeding modes.

- 60. Several experiments have been able to demonstrate a maximum grazing rate allowing for long-term acclimation to food concentration above the incipient limiting level. Values for TZMAX range from 0.045 to 3.44 1/day.
- 61. Dissolved organic matter (DOM) is another potential source of food for zooplankters, although this feeding transfer is not modeled in CE-QUAL-Rl. Values for maximum ingestion rates for zooplankton are given in Table 12.

Table 12
Maximum ingestion rates for zooplankton (1/day)

| PREDATOR              | VALUE | FOOD SOURCE             | REFERENCE                |
|-----------------------|-------|-------------------------|--------------------------|
| Bosmina               | 0.01  | detritus                | Bogdan and McNaught 1975 |
| Brachionus rubens     | 3.438 | Chlorella               | -                        |
| 21 1                  |       | vulgaris                | Pilarska 1977            |
| Cladocerans           | 0.15  | detritus                | Bogdan and McNaught 1975 |
| Copepods              | 0.10  | detritus                | Bogdan and McNaught 1975 |
| Daphnia               | 0.01  | detritus                | Bogdan and McNaught 1975 |
| Daphnia magna         | 0.251 | Saccharomyces           |                          |
| Danhuia magna         | 0.450 | cervisiae               | McMahon and Rigler 1965  |
| Daphnia magna         | 0.452 | Tetrahymena             | W-W-b 1 m' 1 1065        |
| Daphnia magna         | 0.301 | pyriformis<br>Chlorella | McMahon and Rigler 1965  |
| Dapinita magna        | 0.301 | vulgaris                | MaMahan and Dialog 1005  |
| Daphnia magna         | 0.045 | Escherichia             | McMahon and Rigler 1965  |
| Dapiniza magna        | 0.045 | coli                    | McMahon and Rigler 1965  |
| Daphnia magna         | 0.760 | Chlorella               | McManon and Rigier 1965  |
|                       | 000   | vulgaris                | Kersting and Van De      |
|                       |       | · drydrio               | Leeuw-Leegwater 1976     |
| Daphnia magna         | 0.350 | Saccharomyces           | zeedii zeegiideel 1370   |
| •                     |       | cerivisiae              | Rigler 1961              |
| Daphnia magna         | 1.9   | Chlorella               |                          |
| -                     |       | vulgaris                | Ryther 1954              |
| Daphnia magna         | 2.2   | Navicuĺa                | -                        |
|                       |       | pelliculosa             | Ryther 1954              |
| Daphnia magna         | 2.3   | Scenedesmus             | -                        |
|                       |       | quadricauda             | Ryther 1954              |
| Daphnia pulex         | 0.120 | Chlorococcum            |                          |
|                       |       | sp.                     | Monokov and Sorokin 1961 |
| Daphnia rosea         | 0.900 | Rhodotorula             |                          |
|                       |       | glutinis                | Burns and Rigler 1967    |
| Diaptomus             | 0.47  | detritus                | Bogdan and McNaught 1975 |
| The Grant washing the |       |                         |                          |
| IN SITU EXPERIMENTS   |       | •                       |                          |
| Heart Lake, Canada    | 0.801 | Various                 | Haney 1973               |
| Lake Vechten, The     | 0.04  | **. *.                  |                          |
| Netherlands           | 0.24  | Various                 | Gulati 1978              |
| Lake Krasnoye, USSR   | 1.20  | Various                 | Andronikova 1978         |
|                       |       |                         |                          |

#### TZMORT

62. TZMORT is the maximum nonpredatory mortality rate for zooplankton (1/day). Nonpredatory mortality rate may be obtained by measuring total mortality and predatory mortality and subtracting to obtain the difference (a direct approach is to measure mortality rate and eliminate predators altogether). Nonpredatory mortality may be influenced by oxygen concentration, temperature, diet, age, and population density. Nonpredatory mortality rates are normally less than 1 percent per day. Values for maximum nonpredatory mortality rate are given in Table 13.

Table 13
Zooplankton mortality rates (1/day)

| SPECIES                 | TZMORT      | REFERENCE                |
|-------------------------|-------------|--------------------------|
| Calanus helgolandicus   | 0.003-0.048 | Paffenhoffer 1976        |
| Calanus helgolandicus   | 0.024       | Mullin and Brooks 1970   |
| Carnivorous zooplankton | 0.002-0.013 | Petipa et al. 1970       |
| Ceriodaphnia reticulata | 0.0016      | Clark and Carter 1974    |
| Copepod nauplii         | 0.006-0.017 | Petipa et al. 1970       |
| Daphnia galeata         | 0.017       | Hall 1964                |
| Daphnia pulex           | 0.012       | Craddock 1976            |
| Daphnia pulex           | 0.018-0.027 | Frank et al. 1957        |
| Daphnia retrocurva      | 0.001       | Clark and Carter 1974    |
| Daphnia rosea           | 0.001-0.007 | Dodson 1972              |
| Daphnia rosea           | 0.001       | Clark and Carter 1974    |
| Daphnia spp.            | 0.002       | Wright 1965              |
| Diaptomus clavipes      | 0.004-0.155 | Gehrs and Robertson 1975 |
| Diaphanosoma            |             |                          |
| leuchtenbergiana        | 0.001       | Clark and Carter 1974    |
| Omnivorous zooplankton  | 0.010-0.013 | Petipa et al. 1970       |
| Paracalanus sp.         | 0.003-0.006 | Petipa et al. 1970       |
| Rhincalanus nasutus     | 0.006-0.015 | Mullin and Brooks 1970   |
| Simocephalus serrulatus | 0.003       | Hall et al. 1970         |

### ZEFFIC

- 63. ZEFFIC, the zooplankton assimilation efficiency (A/G) (dimensionless), is the proportion of food consumed (G) to food assimilated (A), i.e., food actually absorbed from an individual's digestive system. The assimilation efficiency is used to modify consumption and to determine the quantity of energy entering an individual or population.
- 64. Of the factors affecting assimilation efficiency, the most significant is food type. For herbivores-detrivores, the range in ZEFFIC is wide because these animals often consume foods of varying energy content and digestibility. Among the carnivores, for which food type varies little, A/G ranges between 0.80 and 0.95. Values for zooplankton assimilation efficiency are given in Table 14.

Table 14
Zooplankton assimilation efficiency coefficients (dimensionless)

| SPECIES                 | ZEFFIC    | REFERENCE                         |
|-------------------------|-----------|-----------------------------------|
| Acartia clausi          | 0.66-0.73 | Penchen'-Finenko 1977             |
| Bosmina coregoni        | 0.09-0.77 | Semenova 1974                     |
| Bosmina longirostris    | 0.32-0.31 | Gutel'mackher 1977                |
| Calanus firmarchicus    | 0.48-0.96 | Marshall and Orr 1956             |
| Calamoecia lucase       | 0.63-0.67 | Green 1975                        |
| Ceriodaphnia reticulata | 0.106     | Czeczuga & Bobiatynska-Ksok 1970  |
| Ceriodaphnia reticulata | 0.47-0.73 |                                   |
| Cyclops strennus        | 0.50      | Schindler 1971                    |
| Cyclops vicimus         | 0.80      | Monakov 1972                      |
| Daphnia longispina      | 0.10-0.25 | Monakov & Sorokin 1961            |
| Daphnia longispina      | 0.42      | Monakov 1972                      |
| Daphnia magna           | 0.60-0.84 | Schindler 1968                    |
| Daphnia pulex           | 0.14-0.31 | Richman 1958                      |
| Daphnia schodleri       | 0.60-0.90 | Hayward & Gallup 1976             |
| Daphnia sp.             | 0.08-0.25 | Cohn 1958                         |
| Diaptomus graciloides   | 0.81      | Penchen'-Finenko 1977             |
| Diaptomus graciloides   | 0.45-0.50 | Klekowski & Shushkina 1966        |
| Diaptomus siciloides    | 0.40-0.83 | Comita 1972                       |
| Diaptomus oregonensis   | 0.77      | Richman 1964                      |
| Eurycercus lamellatic   | 0.07-0.32 | Smirnov 1962                      |
| Holopedium gibberrum    | 0.10-0.47 | Gutel'mackher 1977                |
| Leptodora kindtii       | 0.40      | Cummins et al. 1969               |
| Leptodora kindtii       | 0.87      | Hillbricht-Ilkowska & Karabin 197 |
| Macrocyclops albidus    | 0.45-0.50 |                                   |
| Mesocyclops albidus     | 0.20-0.75 | Klekowski & Shushkina 1966        |
| Polyphemus pediculus    | 0.42      | Monokov 1972                      |
| Sida crystallima        | 0.17-0.99 | Monakov 1972                      |
| Simocephalus espinosus  | 0.46      | Sorokin 1969                      |
| Simocephalus vetulus    | 0.31-0.72 | Klekowski 1970                    |
| Simocephalus vetulus    | 0.31-0.72 | Ivanova & Klekowski 1972          |
| 10 herbivores           | 0.476     | Comita 1972                       |

# PREF1, PREF2, PREF3

- 65. All zooplankters are selective feeders resulting from a combination of (a) an organism's mechanical limitations in capturing and processing food items of varying size and configuation, (b) the chemical composition of the food items, and (c) feeding behavior. Food preference is demonstrated if an organism consumes a food item in a proportion different from the food item's relative contribution to the total of all available foods in the environment. If all foods occur at the same concentration, then the preference factors equal the fractions of ingestion contributed by each food compartment. Seasonal abundance of phytoplankton, bacteria, and detritus may be the main factor determining the percent composition of these components in the diets of many zooplankters.
- 66. Filamentous bluegreen algae are generally not considered to be as assimilable as are other algal species. They are seldom found in the guts of zooplankton, because they either are not eaten or are actively rejected. Most species of green algae and diatoms are filtered at about the same rate and digested. However, it is not necessarily the taxonomic position of the alga that makes it suitable or unsuitable as food, but rather the attributes of each algal species such as size, shape, and toxicity.
- 67. Although ample evidence exists to show that detritus is consumed by zooplankton, no evidence exists to show that it is consumed preferentially; rather, detritus is ingested in proportion to its composition in the environment. When detritus is included as a food source in a grazing formulation, it should be given equal ranking with other suitable foods. It should be noted that bacteria that colonize detritus constitute an important source of protein in the diet.

- 68. Filter feeders discriminate among particles on the basis of size, shape, and texture. There are upper and lower limits to the sizes of particles that can be managed by zooplankton feeding appendages. Particles of 0.8  $\mu$  and larger can be retained; an upper limit is related to the size of the animal. Algae that clog the filtering appendages are rejected from them by a claw on the lower abdomen.
- 69. Raptorial feeders can sieze large prey and tear it apart before eating (Ambler and Frost 1974, Brandl and Fernando 1975), but there are limits to the size of prey they capture.
- 70. PREF1 is the preference factor of zooplankton for the ALGAE1 compartment, PREF2 is the preference factor of zooplankton for the ALGAE2 compartment, and PREF3 is the preference factor of zooplankton for the detritus compartment. The food preference factors are dimensionless; the total of the three factors must equal 1. Values for these preference factors are given in Table 15.

Table 15
Food preference factors of zooplankton (dimensionless)

| PREDATOR   | PREF   | PREY  | REFERENCE   |
|--|--|---|---|
| Bosmina Bosmina Cladocerans Cladocerans Cladocerans Copepods Copepods Copepods Daphnia Daphnia Diaptomus Diaptomus | 0.33<br>0.33<br>0.30<br>0.30<br>0.20<br>0.45<br>0.15<br>0.20<br>0.33<br>0.17<br>0.40 | nannoplankton netplankton nannoplankton netplankton bluegreen algae nannoplankton netplankton bluegreen algae nannoplankton bluegreen algae nannoplankton netplankton netplankton | Bogdan and McNaught 197 Bodgan and McNaught 197 Bogdan and McNaught 197 |

#### TZRESP

- 71. TZRESP is the maximum zooplankton respiration rate (1/day). Respiration is the sum of all physical and chemical processes by which organisms oxidize organic matter to produce energy. Respiration rates of aquatic invertebrates usually are estimated directly by monitoring oxygen consumption. By multiplying oxygen consumed times an oxycaloric coefficient (i.e., 4.83 cal/ml 02 (Winberg et al. 1934)) and the energy-to-carbon relation for aquatic invertebrates (i.e., 10.98 cal/mg C (Salonen et al. 1976)), the amount of carbon metabolized can be determined and converted to biomass.
- 72. Conover (1960) has indicated that carnivores have higher respiration rates than herbivores. Values for maximum zooplankton respiration rates are given in Table 16.

Table 16

Zooplankton maximum respiration rates (1/day)

| SPECIES                 | TZRESP   | REFERENCE                               |
|-------------------------|----------|---|
| Bosmina coregoni        | 0.170    | Manuilova 1958                          |
| Bosmina longirostris    | 0.185    | Sushchenya 1958                         |
| Ceriodaphnia reticulata | 0.1850   | Gophen 1976                             |
| Copepoda                | 0.075204 | Bishop, 1968                            |
| Copepod adults          | 0.043131 | Williams 1982                           |
| Copepod copepodites     | 0.054171 | Williams 1982                           |
| Copepod nauplii         | 0.165695 | Williams 1982                           |
| Copepod total           | 0.056183 | Williams 1982                           |
| Daphnia ashlandii       | 0.44774  | Duval and Geen 1976                     |
| Daphnia clavipes        | 0.117165 | Comita 1968                             |
| Daphnia cuculata        | 0.161    | Manuilova 1958                          |
| Daphnia galeata         | 0.13772  | LaRow et al. 1975                       |
| Daphnia hyalina         | 0.179    | Blazka 1966                             |
| Daphnia longispina      | 0.121135 | Tezuka 1971                             |
| Daphnia longispina      | 0.16     | Manuilova 1958                          |
| Daphnia longispina      | 0.146    | Shushkina and Pecen' 1964               |
| Daphnia magna           | 0.085175 | Kersting and                            |
| -                       |          | Van De Leeuw-Leegwater 1976             |
| Daphnia magna           | 0.014    | Sushchenya 1958                         |
| Daphnia oregonesis      | 0.194    | Richman 1964                            |
| Daphnia pulex           | 0.582    | Buikema 1972                            |
| Daphnia pulex           | 0.1819   | Tezuka 1971                             |
| Daphnia septopus        | 0.00818  | Comita 1968                             |
| Daphnia siciloides      | 0.00652  | Comita 1968                             |
| Diaphanosoma brachyurum | 0.272    | Sushchenya 1958                         |
| Diaptomus kenai         | 0.272448 | Duval and Geen 1976                     |
| Leptodora kindtii       | 0.471    | Moshiri et al. 1969                     |
| Leptodora kindtii       | 0.125    | Hillbricht-Ilkowska and<br>Karabin 1970 |
| Simocephalus vetulus    | 0.131    | Sushchenya 1958                         |
| Simocephalus vetulus    | 0.154    | Manuilova 1958                          |
| Simocephalus vetulus    | 0.096201 | Ivanova and Klekowski 1972              |
| Total zooplankton       | 0.063210 | Williams 1982                           |
|                         |          |   |

### ZS2P

- 73. ZS2P is the zooplankton half-saturation coefficient for grazing on algae and detritus (mg/L). It has been found that zooplankton exhibit reduced feeding rates at high food concentrations; the relationship between feeding rate and food concentration has been reported to be curvilinear by a number of investigators (Burns and Rigler 1967, Parsons et al. 1967, McQueen 1970, Frost 1972, Monakov 1972, Gaudy 1974, and Chisholm et al. 1975).
- 74. The most realistic calculation of zooplankton grazing rate is based on their rate of removal of biomass of food (Mullin 1963); therefore, it is important that investigators report results in terms of biovolume or biomass instead of cell number. The method most used to determine ingestion rate is to count prey in controls and experimental chambers after feeding zooplankton. Values for zooplankton HSC are given in Table 17.

Table 17
Zooplankton half-saturation coefficients (mg/L)

| SPECIES               | ZS2P     | REFERENCE            |
|-----------------------|----------|----------------------|
| Bosmina coregoni      | 4.0      | Scavia and Eadie 197 |
| Daphnia magna         | 9.6-15.0 | Scavia and Eadie 197 |
| Daphnia rosea         | 0.16     | Scavia and Eadie 197 |
| Diaptomus oregonensis | 1.6      | Scavia and Eadie 197 |

## ZOOT1, ZOOT2, ZOOT3, ZOOT4

- 75. Values for zooplankton temperature coefficients are given in Table 18.
  - a. ZOOT1 is the lower temperature bound at which metabolism continues to occur. It is generally 0°C.

- $\underline{b}$ . ZOOT2 is the lowest temperature at which processes are occurring near the maximum rate (°C).
- c. ZOOT3 is the upper temperature bounding the range of maximum rates (°C).
- d. ZOOT4 is the upper lethal temperature (°C).

Table 18
Zooplankton temperature coefficients (°C)

| SPECIES                 | ZOOT1 | ZOOT2 | ZOOT3 | ZOOT4 | REFERENCE             |
|-------------------------|-------|-------|-------|-------|-----------------------|
| Calamoecia lusasi       | NA*   | 20    | 24    | NΑ    | Green 1975            |
| Ceriodaphnia reticulata | NA    | 24    | . 27  | NA    | Gophen 1976           |
| Daphnia galeata         | NA    | 20    | 24    | NA    | Burns 1969            |
| Daphnia longispina      | NA    | 16    | 18    | NA    | Nauwerck 1959         |
| Daphnia magna           | NA    | 24    | 26    | 35    | McMahon 1965          |
| Daphnia magna           | NA    | 25    | NA    | NA    | Burns 1969            |
| Daphnia middendorffiana | NA    | 24    | 25    | NA    | Kryutchkova and       |
| •                       |       |       |       |       | Kondratyuk 1966       |
| Daphnia pulex           | NA    | 20    | 24    | NA    | Burns 1969            |
| Daphnia pulex           | NA    | 20    | 24    | NA    | Geller 1975           |
| Daphnia pulex           | NA    | NA    | 25    | NA    | Geller 1975           |
| Daphnia rosea           | NA    | 20    | 24    | NA    | Burns & Rigler 1967   |
| Daphnia rosea           | NA    | 14    | 15    | NA    | Kibby 1971            |
| Daphnia schedleri       | NΑ    | 20    | 22    | NA    | Burns 1969            |
| Daphnia schedleri       | NA    | 20    | 24    | NA    | Hayward & Gallup 1976 |
| Diaptomus sp.           | NA    | 16    | 18    | NA    | Nauwerck 1959         |

<sup>\*</sup> NA = not available.

76. As with the phytoplankton, zooplankton are able to adapt to the ambient temperature with time. This is demonstrable throughout the different regions of the United States and at different times of the year. Zooplankton found in temperate regions of the United States are exposed to lower average temperatures throughout the year and consequently have lower temperature factors (i.e., ZOOT1, ZOOT2, ZOOT3, and ZOOT4) than those found in more southern regions. Again, these values are unavailable from the literature but have been estimated by Leidy and Ploskey (1980) based upon acclimation temperatures (Table 19).

Table 19

Acclimation temperature, upper and lower lethal temperature, and the temperature range for a constant maximum grazing rate for zooplankton exposed to rapid temperature stress (°C)

(from Leidy and Ploskey 1980)

| Accl. |       |        |       |       |
|-------|-------|--------|-------|-------|
| Temp. | ZOOT1 | ZOOT2  | ZOOT3 | ZOOT4 |
| 5     | 0 .   | 5      | 6     | 25    |
| 10    | 0     | 10     | 12    | 30    |
| 15    | 2     | 15     | 18    | 33    |
| 20    | 5     | 20     | 24    | 33    |
| 25    | 7     | 25     | 30    | 34    |
| 29    | 10    | 29     | 34    | 34    |
| 30    | 10    | 30     | 34    | 34    |
| 31    | 12    | 31     | 34    | 34    |
| 34    | 15    | 34     | 34    | 34    |
| 35    |       | lethal |       |       |
|       |       |        |       |       |

Table 20

Daily ration of benthic organisms (from Leidy and Ploskey 1980)

(1/day)

| SPECIES                      | FOOD                       | RATION     | REFERENCE              |
|------------------------------|----------------------------|------------|------------------------|
| NEMATODA                     |                            |            |                        |
| Aphelenchus<br>avenae        | fungal mycelia             | 0.26       | Soyza 1973             |
| Plectus<br>palustris         | Acinetobacter              |            |                        |
| •                            | sp.                        | 6.50       | Duncan et al. 1974     |
| MOLLUSCA                     |                            |            |                        |
| Dreissena<br>polymorpha      | bacteria                   | 0.0112     | Sorokin 1966           |
| Goniobais                    |                            |            |                        |
| clavaeformis                 | aufwucks                   | 0.0124     | Malone and Nelson 1969 |
| ARTHROPODA<br>Hyalella       |                            |            |                        |
| azteca                       | sediments                  | 0.17-1.03  | Hargrave 1970          |
| Pontogammarus<br>robustoides | Cladophora sp.             | 0.00798    | Kititsyna 1975         |
| Pontogammarus robustoides    | Tubifex sp.                | 0.187-1.63 | Kititsyna 1975         |
| PODOCOPA                     |                            |            |                        |
| Chaoborus                    |                            |            |                        |
| flavicans                    | natural phyto-<br>plankton |            |                        |
|                              | population                 | 0.036114   | Kajak and Dusoge 1970  |
| Herpetocypris reptans        | Spirogyra sp.              | 1.28       | Yakovleva 1969         |
| Herpetocypris                |                            | 0.03       | V-11 1060              |
| reptans<br>Herpetocypris     | Zygnema sp.                | 0.93       | Yakovleva 1969         |
| reptans                      | Mougeotia sp.              | 0.93       | Yakovleva 1969         |
| Herpetocypris reptans        | Chironomus                 |            |                        |
| II a was a ka a a wa wai a   | plumosus                   | 0.66       | Yakovleva 1969         |
| Herpetocypris<br>reptans     | Asellus aquaticus          | 0.66       | Yakovleva 1969         |
| Herpetocypris reptans        | fish fry                   | 1.09       | Yakovleva 1969         |
| Procladius<br>choreus        | Chironomidae               | 0.00711    | Kajak and Dusoge 1970  |
|                              | CITTOHOMITUAE              | 0.00711    | Rajak and Dusoge 1970  |
| EPHEMEROPTERA<br>Stenonema   |                            |            |                        |
| pulchellum                   | Navicula minima            | 0.234      | Trama 1972             |
| PLECOPTERA                   |                            |            |                        |
| Acroneuria<br>californica    | Hydropsyche sp.            | 0.002087   | Heiman and Knight 1975 |
|                              | Tarohalome ab.             | 5.00= ,00; |                        |
|                              |                            |            |                        |

#### Benthos

## TBMAX

- 77. TBMAX is the maximum ingestion rate for benthos (1/day) and is measured at food densities above the incipient limiting food concentration. The food source for this compartment is organic sediment; its dominant members for most reservoir benthic communities are the aquatic oligochaetes and Chironomidae. Filter feeders, predators, deposit feeders, and surface grazers are all represented in most benthic communities.
- 78. Daily rations (an approximation of the daily grazing rate) of some benthic species compiled by Leidy and Ploskey (1980) are listed in Table 20. Other values for maximum ingestion rate are given in Table 21.

Table 21

Benthos maximum ingestion rates (1/day)

| SPECIES   | TBMAX  | REFERENCE   |
|---|--|---|
| Acroneuria californica Asellus aquaticus Carnivores Chaoborus flavicans Deposit feeder Hyalella azteca Omnivores Pontagammarus robustiodes Procladius choreus Selective deposit feeder Stenonema pulchellum | 0.00209<br>0.25<br>0.0282<br>0.036114<br>0.111<br>0.17-1.3<br>0.043<br>0.07498<br>0.0711<br>0.05<br>0.2123 | Heiman and Knight 1975 Prus 1972 Bigelow et al 1977 Kajak and Dusoge 1970 Gordon 1966 Hargrave 1970 Bigelow et al. 1977 Kititsyna 1975 Kajak and Dusoge 1970 Bigelow et al. 1977 Trama 1972 |

### TBMORT

79. TBMORT is the nonpredatory mortality rate for benthos (1/day). Leidy and Ploskey (1980), in their review of the literature, show most benthos nonpredatory mortality rates to be between 0.001 and 0.02/day.

## BEFFIC

80. BEFFIC is the assimilation efficiency for benthos (dimensionless). The assimilation efficiency is multiplied by the ingestion rate to obtain an assimilation rate. Values for benthos assimilation efficiency are given in Table 22.

Table 22
Benthos assimilation efficiencies (dimensionless)

| SPECIES                  | VALUE     | REFERENCE                   |
|--------------------------|-----------|-----------------------------|
| Anatopina dijari         | 0.30      | Teal 1957                   |
| Asellus aquaticus        | 0.30      | Klekowski 1970              |
| Asellus aquaticus        | 0.26-0.44 | Prus 1971                   |
| Bandsiola crotchii       | 0.31-0.40 | Winterbourn 1974            |
| Calopsectra dives        | 0.20      | Teal 1957                   |
| Carnivores               | 0.20-0.97 | Lawton 1970                 |
| Gammarus pseudolimnaeus  | 0.10-0.20 | Barlocher and Kendrick 1975 |
| Gammarus pseudolimnaeus  | 0.42-0.75 | Barlocher and Kendrick 1975 |
| Gammarus pseudolimnaeus  | 0.10      | Marchant and Hynes 1981     |
| Gammarus pulex           | 0.30-0.40 | Nilsson 1974                |
| Glossosoma nigrior       | 0.17-0.32 | Cummins 1973                |
| Hedriodiscus             | 0.59      | Stockner 1971               |
| Hyalella azeteca         | 0.05-0.80 | Hargrave 1970               |
| Hydrophilus triangularis | 0.55      | Hallmark and Ward 1972      |
| Lepidostoma              | 0.07-0.12 | Grafius 1973                |
| Lestes sponsa            | 0.36      | Klekowski et al. 1970       |
| Lethocerus americanus    | 0.07      | Guthrie and Brust 1969      |
| Limnodrilus hoffmeisteri | 0.5       | Teal 1957                   |
| Most invertebrates       | 0.5       | Monakov 1972                |
| Potamopyrgres jenkinsi   | 0.04      | Heywood and Edwards 1962    |
| Potomophylax cingulatus  | 0.10-0.30 | Otto 1974                   |
| Pteronarcys scotti       | 0.11      | McDiffett 1970              |
| Pyrrhosoma               | 0.77-0.91 | Lawton 1970                 |
| Simulium                 | 0.57      | McCullough 1975             |
| Stenonema                | 0.52      | Trama 1957                  |
| ricorythodes minutus     | 0.07-0.55 | McCullough 1975             |
| Pubifex tubifex          | 0.5       | Ivlev 1939                  |

### BS2SED

81. BS2SED is the half-saturation coefficient for benthos feeding on organic sediment  $(g/m^2)$ . Leidy and Ploskey (1980), after a thorough review of the literature, wrote that they were unable to find a single reference that documented, in units convertible to carbon, the change in benthic grazing as a function of food concentration. In addition, the value of the coefficient depends on the depth of the sediment being modeled, which is itself a variable. The authors of the present report recommend using values slightly smaller than half the initial condition for the sediment, which is reported in  $g/m^2$ .

### TBRESP

82. TBRESP is the maximum respiration rate for benthos (1/day). Respiration rates are estimated directly by monitoring benthic oxygen consumption by manometric, chemical, or polarographic methods. Values for the respiration rate for benthos are given in Table 23.

Table 23
Maximum respiration rates for benthos (1/day)

| SPECIES                 | TBRESP   | TEMP °C | REFERENCE                         |
|-------------------------|----------|---------|-----------------------------------|
| Acartia                 | 0.129215 | NA*     | Williams 1982                     |
| Ancylus fluviatilis     | 0.035049 | 16      | Berg 1952                         |
| Baetes sp.              | 0.4772   | 10      | Fox et al. 1937                   |
| Bithynia tentaculata    | 0.020    | 13      | Berg & Ockelmann 1959             |
| Bithynia leachi         | 0.031    | 13      | Berg & Ockelmann 1959             |
| Chironomus anthracinus  | 0.005    | 11      | Berg et al. 1962                  |
| Chironomus strenzkei    | 0.1214   | 30      | Plpatzer-Schultz 1970             |
| Chloeon dipterum        | 0.1646   | 10-16   | Fox and Simmonds 1933             |
| Coenis sp.              | 0.075    | 10      | Fox et al. 1935                   |
| Corethra flavicans      | 0.002    | 11      | Berg et al. 1962                  |
| Corycaeus               | 0.051270 | NA      | Williams 1982                     |
| Echyonurus venosus      | 0.1734   | 10      | Fox et al. 1935                   |
| Ephemera simulans       | 0.063    | 20      | Olson and Rueger 1968             |
| Ephemera vulgata        | 0.07219  | 10      | Fox et al. 1935                   |
| Ephemera damica         | 0.09521  | 10      | Fox et al. 1935                   |
| Ephemerella ignita      | 0.24     | 10      | Fox et al. 1935                   |
| Erpobdella oculata      | 0.034    | 20      | Mann 1956                         |
| Erpobdella testacea     | 0.052    | 20      | Mann 1956                         |
| Gammarus pulex          | 0.1012   | NA.     | Fox and Simmonds 1933             |
| Gastropoda, Veliger     | 0.107    | NA      | Williams 1982                     |
| Glossiphonia complanata | 0.044    | 20      | Mann 1956                         |
| Helobdella stagnalis    | 0.052    | 20      | Mann 1956                         |
| Ilyodrilus hammoniensis | 0.0009   | 11      | Berg et al. 1962                  |
| Larvaceans              | 0.014043 | NA      | Williams 1982                     |
| Lumbricillus rivalis    | 0.006    | 11      | Berg et al. 1962                  |
| Lymnaea aricularia      | 0.016    | 13      | Berg & Ockelmann 1959             |
| Lymnaea palustris       | 0.027    | 13      | Berg & Ockelmann 1959             |
| Lymnaea pereger         | 0.023    | 13      | Berg & Ockelmann 1959             |
| Many groups             | 0.000104 | NA      | Olson and Rueger 1968             |
| Myxas glutinosa         | 0.026    | 13      | Berg & Ockelmann 1959             |
| Oligotrichs             | 0.257    | NA      | Williams 1982                     |
| Physa fontinalis        | 0.041    | 13      | Berg & Ockelmann 1959             |
| Piscicola geometra      | 0.088    | 20      | Mann 1956                         |
| Procladius sp.          | 0.002    | 11      |                                   |
| Tintinnids              | 0.245    | NA      | Berg et al. 1962<br>Williams 1982 |
| Tubifex barbatus        | 0.005    | 11      |                                   |
| Tubifex tubifex         | 0.001    | 11      | Berg et al. 1962                  |
| Valvata piscinalis      | 0.041    | 13      | Berg et al. 1962                  |
| - Farametro             | 0.044    | 13      | Berg & Ockelmann 1959             |
|                         |          |         |                                   |

<sup>\*</sup> NA = not available.

# BENT1, BENT2, BENT3, BENT4

- 83. Values for benthos temperature coefficients are given in Table 24.
  - a. BENT1 is the lower temperature bound at which metabolism continues to occur; it is usually 0 °C.
  - b. BENT2 is the lowest temperature at which processes are occurring near the maximum rate.
  - c. BENT3 is the upper temperature bounding the range of maximum rates.
  - d. BENT4 is the upper lethal temperature.

Table 24
Temperature coefficients for benthos metabolism (°C)

| SPECIES   | BENT1  | BENT2    | BENT3     | BENT4    | REFERENCE                |
|---|--------|----------|-----------|----------|--------------------------|
| Asellus aquaticus<br>Gammarus pulex<br>Gammarus | 0<br>0 | 15<br>18 | NA*<br>NA | NA<br>NA | Moore 1975<br>Moore 1975 |
| pseudolimnaeus                                  | 0      | 20       | NA        | NA       | Marchant &<br>Hynes 1981 |

<sup>\*</sup> NA = not available.

## Fish

- 84. CE-QUAL-R1 has three fish compartments for simulating piscivorous, planktivorous, and benthic-feeding assemblages in a reservoir. Since many fish species are omnivorous, however, the weighting procedure for computing composite compartment rates is different from other compartments. A report by Leidy and Jenkins (1977) provides all the information necessary to compute the required composite rate coefficients.
- 85. In the model, the piscivorous fish (compartment 1) feed only on the other two fish compartments. Fish in the second compartment feed on detritus, zooplankton, and the two algal groups; fish in the third compartment feed on

sediment and benthos.

# TFMAX

- 86. TFMAX,1 is the maximum ingestion rate (1/day) for the piscivorous fish compartment. The composite rate for the compartment should be computed based on the mean annual standing crop estimate. Ingestion rates vary as a function not only of species, but also of other factors such as condition or age class; the ingestion rate should reflect these factors by using, for example, average age class estimates.
- 87. TFMAX,2 is the maximum ingestion rate for plank-tivorous fish (1/day). The planktivorous fish consume zoo-plankton, algae, and detritus.
- 88. TFMAX,3 is the maximum ingestion rate for benthic fish (1/day). Benthic-feeding fish ingest both benthos and organic sediment.
- 89. In general, a TFMAX coefficient of 0.01 represents maintenance without growth; 0.04 to 0.05 represents optimum growth efficiency (Leidy and Jenkins 1977).

## FS2BEN, FS2ZOO, FS2FSH

90. To adjust the ingestion rate of fish due to the available food supply, the fishery model uses half-saturation constants; these represent the amount of food present that results in fish ingestion at half the maximum growth rate. It has been suggested that the half-saturation constant be considered to be 5 percent of fish wet body weight consumed per day at 20 °C (Leidy and Jenkins 1977). Five percent of the body weight consumed per day corresponds closely with the food intake rate for optimum efficiency in growth (4 to 5 percent for many species). User's of CE-QUAL-Rl should refer to Leidy and Jenkins (1977) because

of the difficulty in estimating half-saturation coefficients. Estimates of fish half-saturation coefficients are given in Table 25.

- a. FS2BEN is the benthic-feeding fishes' (FISH3) halfsaturation coefficient for benthos and sediment grazing (mg/L).
- <u>b.</u> FS2ZOO is the planktivorous fishes' (FISH2) halfsaturation coefficient for zooplankton, detritus, and algae (mg/L).
- c. FS2FSH is the piscivorous fishes' (FISH1) half-saturation coefficient for feeding on FISH3 and FISH2 (mg/L).

Table 25

Estimated half-saturation coefficients for fish growth (mg/L)

(from Leidy and Jenkins 1977)

| SPECIES   | FOOD TYPE  | VALUE                               | REFERENCE  |
|---|--|-------------------------------------|--|
| Largemouth bass Smallmouth bass Muskellunge Reticulate sculpin Sockeye salmon Channel catfish | minnows minnows minnows midge larvae mixed diet mixed diet | 4.6<br>7.2<br>5.6<br>4.4<br>3.9-7.9 | Thompson 1941<br>Williams 1959<br>Gammon 1963<br>Davis and Warren 1965<br>Brett et al. 1969<br>Andrews and Stickney 1972 |

# F2ALG, F2DET, F2ZOO, F3BEN, F3SED

- 91. Preference factors for fish compartments 2 and 3 are as follows:
  - <u>a.</u> F2ALG is the preference of FISH2 for algae (dimensionless).
  - b. F2DET is the preference of FISH2 for detritus (dimensionless).
  - c. F2ZOO is the preference of FISH2 for zooplankton (dimensionless).
  - d. F3BEN is the preference of FISH3 for benthos (dimensionless).
  - e. F3SED is the preference of FISH3 for sediment (dimensionless).

Information relating to fish preference factors is supplied in Leidy and Jenkins (1977) and is reprinted here in Table 26 below. Unfortunately, the different fish foods are expressed as fractions of the total diet rather than as quantities (i.e. grams) consumed, making preference factors difficult to estimate from this information.

Table 26

Fish food expressed as a fraction of the diet

(from Leidy and Jenkins 1977)

| SPECIES                        | $\underline{\mathtt{PLANT}}$ | DETRITUS | ZOOPL | BENTHOS | FISH    |
|--------------------------------|------------------------------|----------|-------|---------|---------|
| Gizzard shad<br>Threadfin shad | 0.10                         | 0.80     | 0.05  | 0.05    | <u></u> |
| (young) Threadfin shad         | 0.30                         | 0.50     | 0.10  | 0.10    |         |
| (old)                          | 0.30                         | 0.05     | 0.15  | 0.55    | 0.10    |
| Rainbow trout                  | 0.05                         |          | 0.60  | 0.15    |         |
| Brook trout                    |                              |          | 0.90  | 0.05    |         |
| Carp                           | 0.30                         | 0.40     | 0.20  | 0.10    |         |
| Minnows                        | 0.20                         |          | 0.20  | 0.60    |         |
| Carpsuckers                    | 0.15                         | 0.65     | 0.05  | 0.15    |         |
| Suckers                        | 0.15                         | 0.65     | 0.05  | 0.15    |         |
| Hogsuckers                     |                              | 0.80     | 0.05  | 0.15    |         |
| Buffalofish                    | 0.05                         | 0.40     | 0.05  | 0.15    |         |
| Redhorse                       |                              |          | 1.00  |         |         |
| Bullhead                       | 0.10                         | 0.25     | 0.50  |         | 0.15    |
| Catfish                        | 0.27                         | 0.10     |       |         | 0.80    |
| Madtoms                        |                              |          | 0.55  |         | 0.18    |
| Silversides                    |                              |          | 0.20  | 0.80    |         |
| Temperate bass                 |                              |          | 0.20  | 0.10    | 0.70    |
| Sunfish                        | 0.10                         | 0.05     | 0.65  |         | 0.05    |
| Black bass                     |                              |          | 0.08  |         | 0.86    |
| Crappie                        | 0.05                         | 0.05     | 0.20  | 0.15    | 0.55    |
| Perch                          |                              |          | 0.20  | 0.20    | 0.60    |
| Freshwater drum                |                              | 0.08     | 0.58  | -       | 0.34    |

92. An example is given for calculating preference factors for the third fish compartment when actual quantities consumed are known. Suppose a particular species of fish consumes 2 g out of an available 16.0 g of benthos and 0.26 g out of an available 120.0 g of sediment. The preference factor (P) for the ith food category equals

$$P_{i} = (E_{i}/A_{i})/SUM_{i}(E_{i}/A_{i}))$$
 (22)

where

 $E_i$  = the amount of the ith food consumed

 $A_i$  = the amount of the ith food available

For the above examples the preference factors would be

P(benthos) = (2.0/16.0)/0.127166 = 0.983

P(sediment) = (0.26/120.0)/0.127166 = 0.017

## FSHT1, FSHT2, FSHT3, FSHT4

- 93. Upper and lower temperature tolerances for fish ingestion are presented as follows:
  - a. FSHTl is the lower temperature boundary, usually 0 °C, at which metabolism continues.
  - b. FSHT2 is the lowest temperature at which processes are occurring at the maximum rates.
  - c. FSHT3 is the upper temperature bounding the range of maximum rates.
  - d. FSHT4 is the upper lethal temperature.
- 94. For most warmwater species, upper and lower temperature tolerances are similar, the lower limit being reached at 0°C and the upper limit between 33 and 37 °C; the optimum temperature is about 27°C. Coldwater species such as salmonids reach a lower temperature limit at 0°C, but the upper limit is near 25°C; the optimum temperature is about 14°C. Temperature tolerance values and the various acclimation temperatures (ACCL), where available, are given in Table 27.

Table 27

Temperature coefficients for fish ingestion (°C)

(from Leidy and Jenkins 1977)

| SPECIES              | ACCL     | FSHT1      | FSHT2 | FSHT3 | FSHT4 | REFERENCE                  |
|----------------------|----------|------------|-------|-------|-------|----------------------------|
| Pickerals            |          | 0          |       | 24    | 34.4  | Leidy and Jenkins 1977     |
| Minnows              |          | 0          | 27    |       | 33.4  | Leidy and Jenkins 1977     |
| Catfish              |          | 0          | 30    |       | 37.1  | Leidy and Jenkins 1977     |
| Sunfish              |          | 2.5        | 27.5  |       | 35.7  | Leidy and Jenkins 1977     |
| Black bass           |          | 1.6        | 27    |       | 36.5  | Leidy and Jenkins 1977     |
| Crappie              |          |            | 23    |       | 32.5  | Leidy and Jenkins 1977     |
| Yellow perch         |          | 0          | 24.2  |       | 30.9  | Leidy and Jenkins 1977     |
| Yellow perch         |          |            |       | 29    |       | Schneider 1973             |
| Fingerling salmon    |          |            | 15    |       |       | Brett et al. 1969          |
| Bluntnose minnow     | 5        |            |       |       | 26.0  | Hart 1947                  |
| Bluntnose minnow     | 10       |            |       |       | 28.3  | Hart 1947                  |
| Bluntnose minnow     | 15       | 1.0        |       |       | 30.6  | Hart 1947                  |
| Bluntnose minnow     | 20       | 4.2        |       |       | 31.7  | Hart 1947                  |
| Bluntnose minnow     | 25       | 7.5        |       |       | 33.3  | Hart 1947                  |
| Flathead minnow      | 10       |            |       |       | 28.2  | Hart 1947                  |
| Flathead minnow      | 20       | 1.5        |       |       | 31.7  | Hart 1952                  |
| Flathead minnow      | 30       | 10.5       |       |       | 33.2  | Hart 1952                  |
| Creek chub           | 5        | 2015       |       |       | 24.7  | Hart 1952                  |
| Creek chub           | 10       |            |       |       | 27.3  | Hart 1952                  |
| Creek chub           | 15       |            |       |       | 29.3  | Hart 1952                  |
| Creek chub           | 20       | 0.7        |       |       | 30.3  | Hart 1952                  |
| Creek chub           | 25       | 4.5        |       |       | 30.3  | Hart 1952                  |
| Chub                 | 14       | 1.5        |       |       | 27.1  | Black 1953                 |
| Finescaled sucker    | 14       |            |       |       | 26.9  | Black 1953                 |
| White sucker         | 25       |            |       |       | 31.2  | Brett 1944                 |
| White sucker         | 5        |            |       |       | 26.3  | Hart 1947                  |
| White sucker         | 10       |            |       |       | 27.7  | Hart 1947                  |
| White sucker         | 15       |            |       |       | 29.3  | Hart 1947                  |
| White sucker         | 20       | 2.5        |       |       | 29.3  | Hart 1947                  |
| White sucker         | 25       | 6.0        |       |       | 29.3  | Hart 1947                  |
| White sucker         | 23       | 0.0        | 27    |       | 29.3  | McCormick and Mischuk 1973 |
| Brown bullhead       | 5        |            | 2,    |       | 27.8  | Hart 1952                  |
| Brown bullhead       | 10       |            |       |       | 29.0  | Hart 1952                  |
| Brown bullhead       | 15       |            |       |       | 31.0  | Hart 1952                  |
| Brown bullhead       | 20       |            |       |       | 32.5  |                            |
| Brown bullhead       | 25       |            |       |       | 33.8  |                            |
| Brown bullhead       | 30       |            |       |       | 34.8  | Hart 1952<br>Hart 1952     |
| Brown bullhead       | 34       |            |       |       |       |                            |
| Black bullhead       | 23       |            |       |       | 34.8  | Hart 1952                  |
| Channel catfish      | 25<br>25 |            |       |       | 35    | Black 1953                 |
| Channel catfish      | 35       |            |       |       | 35.5  | Allen and Strawn 1968      |
| Channel catfish      | 33       |            | 3.0   |       | 38    | Allen and Strawn 1968      |
|                      | 7 F      | 0.0        | 18    |       | 20.0  | Andrews and Stickney 1972  |
| Channel catfish      | 15       | 0.0        |       |       | 30.3  | Hart 1952                  |
| Channel catfish      | 20       | 2.5        |       |       | 32.8  | Hart 1952                  |
| Channel catfish      | 25       | 6.0        |       |       | 33.5  | Hart 1952                  |
| Bluegill             | 15       | 2.5        |       |       | 30.7  | Hart 1952                  |
|                      |          |            |       |       |       |                            |
| Bluegill<br>Bluegill | 20<br>25 | 5.0<br>7.5 |       |       | 31.5  | Hart 1952<br>Hart 1952     |

Table 27 (concluded)

| SPECIES            | ACCL | FSHT1 | FSHT2 | FSHT3 | FSHT4 | REFERENCE                |
|--------------------|------|-------|-------|-------|-------|--------------------------|
| Bluegill           | 30   | 11.1  |       |       | 33.8  | Hart 1952                |
| Bluegill           |      |       | 22    |       | 33.8  | McComish 1971            |
| Longear sunfish    | 25   |       |       |       | 35.6  | Neill et al. 1966        |
| Longear sunfish    | 30   |       |       |       | 36.8  | Neill et al. 1966        |
| Longear sunfish    | 35   |       |       |       | 37.5  | Neill et al. 1966        |
| Pumkinseed         | 25   |       |       |       | 24.5  | Brett 1944               |
| Smallmouth bass    | 35   | 1.6   | 26.3  |       | 35.0  | Horning and Pearson 1973 |
| Smallmouth bass    |      |       | 28.3  |       |       | Peck 1965                |
| Largemouth bass    |      |       | 27.5  | 30    |       | Strawn 1961              |
| Largemouth bass    |      |       | 25    |       |       | Niimi and Beamish 1974   |
| Largemouth bass    | 20   | 5.5   |       |       | 32.5  | Hart 1952                |
| Largemouth bass    | 25   |       |       |       | 34.5  | Hart 1952                |
| Largemouth bass    | 30   | 11.8  | •     |       | 36.4  | Hart 1952                |
| Yellow perch       | 5    |       |       |       | 21.3  | Hart 1947                |
| Yellow perch       | 10   | 1.1   |       |       | 25.0  | Hart 1947                |
| Yellow perch       | 15   |       |       |       | 27.7  | Hart 1947                |
| Yellow perch       | 25   | 3.7   |       |       | 29.7  | Hart 1947                |
| Yellow perch-      |      |       |       |       |       |                          |
| juvenile           | 24   |       | 20    | 23.3  |       | McCauley and Read 1973   |
| Yellow perch-      |      |       |       |       |       | <del>-</del>             |
| adult              | 24   |       | 17.6  | 20.1  |       | McCauley and Read 1973   |
| Yellow perch       | 8    |       | 18.6  |       |       | Ferguson 1958            |
| Yellow perch       | 10   |       | 19.3  |       |       | Ferguson 1958            |
| Yellow perch       | 15   |       | 23.0  |       |       | Ferguson 1958            |
| Yellow perch       | 20   |       | 23.1  |       |       | Ferguson 1958            |
| Yellow perch       | 25   |       | 24.5  |       |       | Ferguson 1958            |
| Yellow perch       | 30   |       | 26.7  |       |       | Ferguson 1958            |
| Sockeye salmon-fry | 5    | 0     |       |       | 22.2  | Brett 1952               |
| Sockeye salmon-fry | 10   | 3.1   |       |       | 23.4  | Brett <b>19</b> 52       |
| Sockeye salmon-fry | 15   | 4.1   |       |       | 24.4  | Brett 1952               |
| Sockeye salmon-fry | 20   | 4.7   |       |       | 24.8  | Brett 1952               |
| Sockeye salmon-    |      |       |       |       |       |                          |
| juvenile           | 15   |       | 15    | 17    |       | Brett et al. 1969        |
| Coho salmon        | 5    | 0.2   |       |       | 20.9  | Brett 1952               |
| Coho salmon        | 10   | 1.7   |       |       | 23.7  | Brett 1952               |
| Coho salmon        | 15   | 3.5   |       |       | 24.3  | Brett 1952               |
| Coho salmon        | 20   | 4.5   |       |       | 25.0  | Brett 1952               |
| Chinook salmon     |      |       | 18.4  |       |       | Olson and Foster 1955    |
| Northern pike      | 25   |       |       |       | 32    | Scott 1964               |
| Lake trout         |      |       | 11.7  |       |       | McCauley and Tait 1970   |
| Lake trout         |      |       | 8     | 10.9  |       | Rawson 1961              |
| Rainbow trout      | 18   |       | 17    | 20    |       | McCauley and Pond 1971   |
| Brook trout        | 5    |       |       |       | 23.7  |                          |
| Brook trout        | 10   |       |       |       | 24.4  |                          |
| Brook trout        | 15   |       |       |       | 25.0  | Fry et al. 1946          |
| Brook trout        | 20   |       |       |       | 25.3  | Fry et al. 1946          |
| Brook trout        | 25   | 0.5   |       |       | 25.3  | Fry et al. 1946          |
| Brook trout        |      |       | 14    | 19    |       | Graham 1949              |

### FEFFIC

95. FEFFIC, the assimilation efficiency for fish (dimensionless), ranges from 0.66 to 0.98; a value of 0.80 is realistic for most fish (Leidy and Jenkins 1977). The assimilation efficiency is multiplied by the ingestion rate to obtain an assimilation rate. Values for fish assimilation efficiency are given in Table 28.

Table 28
Assimilation efficiencies of fish (dimensionless)

| SPECIES  | FEFFIC   | REFERENCE   |
|--|--|---|
| Carnivorous fish Carp Carp Cichlasoma bimaculatum Cutthroat trout Ctenopharyngodon Dace Goldfish Green sunfish | 0.80<br>0.80<br>0.80<br>0.97<br>0.80<br>0.74<br>0.95<br>0.69-0.89<br>0.84-0.86<br>0.14<br>0.79<br>0.71-0.86<br>0.94<br>0.94-0.97<br>0.72<br>0.35<br>0.79<br>0.74-0.84<br>0.78<br>0.66-0.69 | Mann 1965 Burbridge 1974 Pierce and Wissing 1974 Gerking 1955 Wingerg 1956 Ivlev 1939a Kobashi and Deguchi 1971 Warren and Davis 1967 Krokhin 1959 Fisher 1970 Mann 1965 Davies 1964 Gerking 1952a Gerking 1952a Johnson 1966 Klekowski et al. 1970 Mann 1965 Davis and Warren 1965 Mann 1965 |

#### TFMORT

96. TFMORT is the nonpredatory mortality rate for fish (1/day). Mortality rate is that fraction of fish biomass that is converted to detritus by death. Nonpredatory mortality rates can be highly variable depending on species, age, exploitation rate, and numerous environmental variables.

The average rate calculated by Leidy and Jenkins (1977) is 0.001 for exploited populations.

97. Ricker (1945) has reviewed techniques for calculating various mortality rates (total, instantaneous, conditional, natural, and fishing). Values for nonpredatory mortality are given in Table 29.

Table 29
Fish nonpredatory mortality rates (1/day)

| SPECIES         | TFMORT    | REFERENCE                  |
|-----------------|-----------|----------------------------|
| American shad   | 0.002     | Walburg 1961               |
| Bluegill        | 0.002     | Patriarche 1968            |
| Bluegill        | 0.0002    | Gerking 1952b              |
| Bluegill        | 0.001     | Ricker 1945                |
| Brook trout     | 0.001     | Latta 1962                 |
| Brook trout     | 0.003004  | Alexander and Shetter 1961 |
| Brook trout     | 0.56-1.34 | Hatch and Webster 1961     |
| Brown bullhead  | 0.001     | McCammon and Seeley 1961   |
| Brown bullhead  | 0.001     | Rawstron 1967              |
| Channel catfish | 0.001     | Ricker 1958                |
| Cutthroat trout | 0.001002  | Hansen 1971                |
| Cutthroat trout | 0.001     | Ball and Cope 1961         |
| Freshwater drum |           | Butler 1965                |
| Largemouth bass | 0.00037   | Mraz and Threinen 1955     |
| Longnose sucker | 0.002     | Geen et al. 1966           |
| Northern pike   | 0.002     | Groebner 1960              |
| Northern pike   | 0.002     | Johnson and Peterson 1955  |
| Rock bass       | 0.002     | Ricker 1947                |
| Walleye         | 0.001     | Olson 1957                 |
| White catfish   | 0.001     | McCammon and Seeley 1961   |

#### TFRESP

98. TFRESP is the fish respiration rate (1/day). There are three types of respiration that can be defined:
(a) standard respiration—oxygen consumed in the absence of measurable movement (i.e., nonactive respiration, basal of resting metabolism), (b) routine respiration—rate of

oxygen consumption of fish showing normal activity, and (c) active respiration—maximum rate of oxygen consumption under continuous forced active respiration. It would appear that the best estimates of the rate of respiration for normal active fish are values for routine metabolism (i.e., type 2 above) (Winberg 1956). Values for fish respiration rate are given in Table 30.

Table 30

Fish maximum respiration rates (1/day)

| SPECIES   | TFRESP                                    | $	ext{TYPE}$                              | REFERENCE   |
|---|---|---|---|
| Brown bullhead Brook trout Carp Lake trout Rainbow trout Salvelinus | 0.001<br>0.003<br>0.001<br>0.001<br>0.002 | routine routine routine standard standard | Beamish 1964 Beamish 1964 Beamish 1964 Gibson and Fry 1954 Florke et al. 1954 |
| fontinalis<br>Salvelinus  | 0.006024                                  | standard                                  | Madsen et al. 1977  |
| fontinalis<br>Sockeye salmon<br>White sucker                        | 0.019101<br>0.002<br>0.002                | active<br>standard<br>routine             | Madsen et al. 1977<br>Brett 1944<br>Beamish 1964                              |

# Other Coefficients

## TDSETL

99. TDSETL is the detrital settling velocity (m/day). Detrital settling velocities vary from 0.001 to over 200 m/day depending on the detrital characteristics and reservoir hydrodynamics. Settling rates should be obtained from quiescent settling chamber studies because advective and turbulent forces in the mixed layer that can reduce settling in a reservoir are modeled separately. For most studies, settling velocities are in the range of 0.05 to 1.0 m/day.

Much higher values are often reported for fecal pellets, as shown in Table 20; however, such high settling coefficients may be questionable because they produce unrealistically low detritus values in the modeling studies. Values for detritus settling velocities are given in Table 31.

Table 31
Detritus settling velocities (m/day)

|                           | <del></del> |                       |
|---------------------------|-------------|-----------------------|
| SOURCE                    | TDSETL      | REFERENCE             |
| Ceratium balticum         | 9.0         | Apstein 1910          |
| Chaetoceros borealis      | 5.0         | Apstein 1910          |
| Chaetoceros didymus       | 0.85        | Eppley et al. 1967b   |
| Cricosphaera carterae     | 1.70        | Eppley et al. 1967b   |
| Ditylum brightwellii      | 2.0         | Apstein 1910          |
| Fecal pellets:            |             |                       |
| Acartia clausii           | 116.0       | Smayda 1971           |
| Fecal pellets:            |             |                       |
| Euphausia krohnii         | 240.0       | Fowler and Small 1972 |
| Fecal pellets:            |             |                       |
| Eupĥausia pacifica        | 43.0        | Osterberg et al. 1963 |
| Fecal pellets:            |             |                       |
| Pontella meadii           | 54.0-88.0   | Turner 1977           |
| Phaeodactylum tricornutur | m 0.0204    | Riley 1943            |
| Rhizosolenia herbetata    | 0.22        | Eppley et al. 1967b   |
| Stephanopyxis tunis       | 2.1         | Eppley et al. 1967b   |
| Tabellaria flocculosa     | 0.46 - 1.5  | Smayda 1971           |
| Thalassiosira psuedonana  | 0.85        | Hecky and Kilham 1974 |
| -                         |             |                       |

## DETT1, DETT2

- 100. DETT1 is the lower temperature boundary at which decomposition continues to occur. It is usually 0 °C.
- 101. DETT2 is the temperature at which decomposition occurs near the maximum rate. Temperature coefficients for decomposition are given in Table 32.

Table 32

Temperature coefficients for decomposition (°C)

| SUBSTRATE OR SITE   | DETT1  | DETT2                | REFERENCE   |
|---|--------|----------------------|---|
| Pseudomonas fluorescens:     natural substrate E. coli: natural | 0      | 25-30                | Tison and Pope 1980                                     |
| substrate<br>Glucose: Lake George,                              | 0      | 37                   | Tison and Pope 1980                                     |
| New York Glucose Glucose: Lake Wingra, Wis.                     | 0<br>0 | 25<br>20-30<br>25-30 | Tison et al. 1980<br>Bott 1975<br>Boylen and Brock 1973 |

#### TDOMDK

- 102. TDOMDK is the dissolved organic matter (DOM) decay rate (1/day). DOM in natural waters is the organic substrate for heterotrophic metabolism. The composition of natural DOM is highly variable and little understood, but its sources are generally grouped into (a) excretion from phytoplankton and macrophytes, (b) decomposition of phytoplankton and macrophytes, (c) excretion by animals, and (d) allochthonous drainage (e.g., humic compounds from upstream sources).
- 103. Aquatic bacteria appear to be chiefly responsible for the removal of DOM compounds from the water; they are the major agents for bacterial mineralization of organic solutes in fresh water (Wright 1975), using organic matter as an energy source. Various methods have been tested to determine the decay rate of DOM in water. Modification of the basic Parson and Strickland (1963) technique have been developed to quantify the kinetics.
- 104. DOM decomposition rates have also been represented by filtered carbonaceous biochemical oxygen demand (BOD) decay rates. If sufficient oxygen is available, the

aerobic biological decomposition of organics will continue until all the DOM is consumed. In the standard test for BOD, a sample is diluted with water containing a known amount of oxygen. The loss of oxygen after the sample has been incubated for 5 days at 20 °C is known as the 5-day BOD. The value of the first-order decay rate is generally about 0.05 to 0.20 per day.

105. The BOD test suffers from several serious deficiencies. The test has no stoichiometric validity, for example: the arbitrary 5-day period usually doesn't correspond to the point where all the organic matter is consumed.

106. Contributing to the errors involved in measuring decay rates of DOM is the extensive variability in the composition and stage of decomposition of DOM. Allochthonous inputs of DOM are likely to be more refractory than autochthonous inputs, and as a result, decomposition rates will be slower and decay may be incomplete; therefore, the length of time the organic matter is available for decomposition is important. In addition, as particles sink out of the euphotic zone, both dissolved and detrital organic substrates may be limited to more resistant fractions thereby arresting attached microbial growth. Therefore, the rate of DOM decomposition may be lower in the hypolimnion of a stratified reservoir.

107. Oxygen consumption rate (mg 02/L/hr) can be transformed into a mineralization rate of organic carbon (mg C/L/hr) by application of a conversion factor of 0.29 (Seepers 1981). Values for DOM decay rate are given in Table 33.

Table 33
DOM decay rates (1/day)

| COMPOUND  | TDOMDK  | REFERENCE  |
|---|---|--|
| Acetate Amino acids Glucose Glucose Glucose Glucose Glutamate Glycine Glycine Glycolate Glycolate Glycolate Glycolic acid | 0.2<br>0.64<br>0.24<br>0.3250<br>0.111<br>0.11625<br>0.31245<br>0.048<br>0.024432<br>0.01225<br>0.004 | Wright 1975 Williams et al. 1976 Williams et al. 1976 Toerien and Cavari 1982 Wright 1975 Carney and Colwell 1976 Vaccaro 1969 Vaccaro 1969 Wright 1975 Wright 1975 Tanaka et al. 1974 |

#### TNH3DK

- 108. TNH3DK is the ammonia decay rate (i.e., the rate at which ammonia is oxidized to nitrite) (1/day). Ammonia is generated by heterotrophic bacteria as the primary end product of decomposition of organic matter, either directly from proteins or from other nitrogenous organic compounds. Although ammonia is a major excretion product, this nitrogen source is minor in comparison to decomposition.
- 109. Nitrification is the biological conversion of organic and inorganic N compounds from a reduced state to a more oxidized state (Alexander 1965). The nitrifying bacteria capable of oxidation of NH4+ to NO2- are largely confined to the species <u>Nitrosomonas</u>, bacteria which are mesophilic (1-37 °C).
- 110. Nitrification rate can be determined by a number of different techniques. Courchaine (1968) has plotted nitrogenous BOD on a logarithmic scale and determined the decay rate from the slope of the line. Thomann et al. (1971) used a finite-difference approximation to solve a

set of simultaneous linear equations.

- 111. Laboratory measurements for the ammonia decay rate can produce results that differ from what might be measured in <u>situ</u>. Several environmental factors influence the rate of nitrification, including pH, temperature, suspended particulate concentration, hydraulic parameters and benthos.
- 112. Nitrification can be measured as a one- or twostep process. In the one-step method, only the end product
  of the entire reaction, nitrate, is measured. In the twostep method, (a) nitrite accumulation is measured as ammonia
  is oxidized to nitrite and (b) nitrate accumulation is
  measured as nitrite is oxidized to nitrate. Oxidation of
  ammonia to nitrite is the rate-limiting step in the total
  reaction; therefore, experiments that measure the rate of
  the total reaction (i.e., the one-step method) can be used
  to estimate this parameter. Ammonia oxidation rates are
  given in Table 34.

Table 34
Ammonia oxidation rates (1/day)

| SITE  | TNH3DK  | REFERENCE  |
|---|---|--|
| Wastewater treatment plant Grand River, Ill. Grasmere Lake, U.K. Truckee River, Nev. Upper Mohawk River, N.Y. Middle Mohawk River Lower Mohawk River Ohio River Big Blue River, Neb. Flint River, Mich. | 0.05-0.30<br>0.80<br>0.001013<br>0.09-1.30<br>0.23-0.40<br>0.30<br>0.30<br>0.25<br>0.17-0.25<br>0.76-0.95 | Wild et al. 1971 Bansal 1976 Hall 1982 Bansal 1976 |

#### TNO2DK

113. TNO2DK is the decay rate of nitrite to nitrate (1/day).

#### TDETDK

- 114. TDETDK is the detritus decay rate (1/day). Detritus as defined by Wetzel et al. (1972) consists of organic carbon lost from an organism by nonpredatory means (including egestion, excretion, secretion, etc.) from any trophic level component, or input from sources external to the ecosystem that enter and cycle in the system (i.e., allochthonous organic carbon). For CE-QUAL-R1, this should be considered to be particulate material only.
- The rate of detritus decay can be determined by measuring the use of oxygen during decomposition, with results expressed as a first-order decay coefficient (k base e = mg oxygen used/mg/day). Many workers have measured rates of oxygen uptake by detritus, suggesting that oxygen uptake is related to the organic matter available for decomposition. Odum and de la Cruz (1967) and Fenchal (1970), for example, demonstrated an inverse relation between detritus particle size and oxygen consumption. Oxygen uptake is an integrative measure of all oxidative processes occurring in the sample, both chemical and biological: reducing substances are usually rapidly oxidized; respiration of the organisms associated with detritus is primarily bacterial, although algae, protozoa, and fungi may also contribute. Measurement of the oxygen uptake reflects the metabolism of communities of microorganisms involved in the decomposition of natural substances.
- 116. As a detrital particle decomposes with time, there is a decline in oxygen uptake accompanied by succession of communities of microorganisms; this decline occurs

as the matter changes from labile to refractory; refractory matter often accumulates in the sediment. Rates of decay are generally high initially and slow down as the material becomes refractory; the rate is influenced by temperature, detrital composition, and age of the detritus. Macrophyte communities are the primary source of detritus in most Submersed and floating macrophytes generally decay more rapidly than the highly lignified emergent species. Particulate organic matter of dead bluegreen algae decomposes much faster than that derived from green algae diatoms and desmids. Particulate organic matter (POM) is especially resistant (Gunnison and Alexander 1975). As detritus decays, there is a decrease in the C:N ratio as a result of a buildup of microbial protein (Mann 1972). A 1-g sample of detritus at 20 °C consumes about 1 mg oxygen/ hr (Hargrave 1972).

- 117. Plant litter consists of a variety of compounds (i.e., sugars, hemicellulose, lignin, waxes) which decay at different rates. The decay curves initially tend to follow the exponential decay functions of the more readily degradable fractions, particularly aquatic macrophytes, which account for a large proportion of the weight of plant litter; therefore, the majority of the litter's weight loss occurs in the first year. Over the long term, the decay rates change, especially for deciduous leaf litter which has a larger proportion of decay-resistant material than do aquatic macrophytes and therefore decays at a much slower rate.
- 118. Decay rates can also be measured by suspending a nylon mesh bag of detrital material in situ or under controlled conditions and determining weight loss with time. This actually measures weight loss due to enzymatic decomposition by bacteria and fungi, solution of soluble sub-

stances, and loss of fragments through the container pores.

- 119. Decay rates have also been determined by measuring the mineralization rates of carbon, nitrogen, and phosphorus (Otuski and Hanya 1972). Decomposition of detritus generated from planktonic communities of surface lake water occurs at rates on the order of 10 percent per day (Saunders 1972), based upon radioactive carbon tracer studies.
- 120. Consideration should be given to the primary or expected sources of detritus. Decomposition rates for allochthonous detrital sources are generally lower than for autochthonous sources to reflect the more refractory nature of allochthonous material after its transport through the upper portions of the reservoir. While a one-dimensional model like CE-QUAL-Rl assumes instantaneous dispersal of inflow constituents, much of the decomposition in the prototype reservoir system occurs in the headwater area. labile fraction of autochthonous detritus produced in the pelagic zones of the lower reservoir will decompose more rapidly in the water column and should have a higher decomposition rate than allochthonous detritus. However, in a stratified reservoir the POM in the hypolimnion may not be exchanged with the epilimnetic waters. The POM becomes more refractory with time, and rates of decomposition decrease.
- 121. Microbial decomposition of detritus can be represented by three stages: a very quick solution of soluble organic components, a relatively rapid decomposition of labile organic constituents, and slow decomposition of refractory organic constituents. Detritus decay rates are given in Table 35.

Table 35
Detritus decay rates (1/day)

| DETRITUS SOURCE  | TDETDK   | REFERENCE  |
|--|--|--|
| Beech Cladophera glomerata Dead green algae Dead mixed algae Dead mixed algae Gloeotrichia | 0.001004<br>0.007<br>0.016076<br>0.007111<br>0.00706 | Hanlon 1982<br>Piecznska 1972<br>Otsuki and Hanya 1972<br>Jewell and McCarty 1971<br>Fitzgerald 1964       |
| echinulata Isoetes lancustris Leaf packs Osier Potamogeton crispus Potomogeton perfoliatus | 0.001005<br>0.002004                                 | Piecznska 1972<br>Hanlon 1982<br>Sedell et al. 1975<br>Hanlon 1982<br>Rogers and Breen 1982<br>Hanlon 1982 |

#### TCOLDK

TCOLDK is the coliform decay rate (1/day). timates of coliform die-off rates may be obtained in the laboratory or in situ. In situ, where there are no flow regime data, or where flows are of a transient nature, a commonly used method is to add a slug of a conservative tracer substance (a dye, rare element, or radioisotope) to steady-state discharge. The discharge plume is sampled, dilution is estimated from the concentration of tracer, and the decay rate is estimated from the dilution-corrected coliform counts. This technique gives misleading results in cases where the tracer is diluted by water heavily contaminated with the same discharge. Since the tracer was introduced as a slug, there is no way to know how many of the surviving coliforms originated in the tracer-dosed effluent and how many came from pre- or post-dosing efflu-This problem is reduced where the flow regime is sufficiently stable (Zison et al. 1978).

- 123. There are two approaches to estimating die-off rates. Frost and Streeter (1924) were able to estimate the die-off rate using seasonal averages of coliform counts from a downstream station, by assuming plug flow in the river. Errors in the rates determined by this approach are attributable to (a) dilution and to longitudinal mixing that produced overestimates and (b) unconsidered sources of coliforms that produced underestimates.
- 124. In a second approach, a mathematical model of the flow and mixing in the system is used to correct the measurements for the effects of dilution. In this manner Marais (1974) analyzed coliform die-off in wastewater maturation ponds as a first-order decay reaction in a series of completely mixed steady-state reactors. Errors in the decay rates determined in this way are primarily attributable to the reliability of the system model.
- 125. Table 36 gives decay rates for coliform and fecal streptococcus. In Table 37 from Mitchell and Chamberlain (1978), the median die-off value was 0.040/hr for freshwater coliform. In general, the die-off follows first-order decay kinetics, although a significant increase in coliform levels is commonly observed in the first several miles downstream from the outfall.
- 126. Factors affecting coliform decay rate include sedimentation, solar radiation, nutrient deficiencies, predation, algae, bacterial toxins, and physiochemical factors.

Table 36
Coliform and fecal streptococcus decay rates (1/day)

| SPECIES  | TCOLDK   | REFERENCE   |
|--|--|---|
| Fecal coliform Fecal streptococci Fecal streptococci Total coliform | 0.199696<br>1.99<br>0.168-1.56<br>0.009028<br>0.021038<br>0.045049<br>0.024105 | Kittrell and Furfari 1963<br>Klock 1971<br>Marais 1974<br>Geldreich et al. 1968<br>Klock 1971<br>Evans et al. 1968<br>Frost and Streeter 1924 |

Table 37

Freshwater die-off rates of coliform bacteria measured in situ (1/day)

(from Mitchell and Chamberlain 1978)

| SITE                     | TEMP/SEASON | RATE  | REFERENCE                 |
|--------------------------|-------------|-------|---------------------------|
| Ohio River               | Summer 20°C | 1.175 | Frost and Streeter 1924   |
| Ohio River               | Winter 5°C  | 1.08  | Frost and Streeter 1924   |
| Upper Illinois River     | June-Sept.  | 2.04  | Hoskins et al. 1927       |
| Upper Illinois River     | OctMay      | 2.52  | Hoskins et al. 1927       |
| Upper Illinois River     | Dec. Mar.   | 0.576 | Hoskins et al. 1927       |
| Upper Illinois River     | AprNov.     | 1.032 | Hoskins et al. 1927       |
| Lower Illinois River     | June-Sept.  | 2.04  | Hoskins et al. 1927       |
| Lower Illinois River     | OctMay      | 0.888 | Hoskins et al. 1927       |
| Lower Illinois River     | DecMar.     | 0.624 | Hoskins et al. 1927       |
| Lower Illinois River     | AprNov.     | 0.696 | Hoskins et al. 1927       |
| Shallow turbulent        |             |       |                           |
| stream                   | Summer      | 15.12 | Kittrell and              |
|                          |             |       | Koschtitzky 1947          |
| Missouri River           | Winter      | 0.48  | Kittrell and Furfari 1963 |
| Tennessee River          |             |       |                           |
| (Knoxville)              | Summer      | 1.03  | Kittrell and Furfari 1963 |
| Tennessee River          |             |       |                           |
| (Chattanooga)            | Summer      | 1.32  | Kittrell and Furfari 1963 |
| Sacramento River, Calif. | Summer      | 1.752 | Kittrell and Furfari 1963 |
| Cumberland River, Md.    | Summer      | 5.52  | Kittrell and Furfari 1963 |
| Groundwater stream       | 10°C        | 0.504 | Wuhrmann 1972             |
| Leaf River, Miss.        | NA          | 0.408 | Mahloch 1974              |
| Wastewater lagoon        | 7.9-25.5°C  |       |                           |
| Maturation ponds         | NA          | 1.99  | Marais 1974               |
| Maturation ponds         | 19°C        | 1.68  | Marais 1974               |
| Oxidation ponds          | 20°C        | 2.59  | Marais 1974               |
|                          |             |       |                           |

#### TSEDDK

127. TSEDDK is the organic sediment decomposition rate (1/day). While sediment consists primarily of settled organic detritus, the decomposition rate should reflect the changing nature of the detritus as it reaches the sediment; i.e., it becomes more refractory since the labile portion of the organic detritus decomposes as it settles through the water column. In addition, since the initial value for sediment is in  $g/m^2$ , the thickness of the sediment layer, along with TSEDDK, will affect the amount of predicted decomposition. Thus, if high initial values are used for sediment, TSEDDK may have to be lowered since only the top few centimeters of sediment are usually involved in aerobic decomposition. Hargrave (1969) found the following relationship between the rate of oxygen comsumption by sediments  $(m1 \ 02/m^2/hr)$  and the temperature  $(T, ^{\circ}C)$ :

 $\ln (O_2 \text{ consumption rate}) = 1.74*\ln(T)-1.30$  (23)

At 6° C this would be 214.3 mg  $02/m^2/day$ , assuming a constant rate for the day and the conversion formula found in the CE-QUAL-R1 User's Manual (Environmental Laboratory 1982, p. 188). At 25° C the rate would be 2567 mg/m²/day. The amount of sediment (in mg/m²) times the value for TSEDDK times 1.4 (i.e., the stoichiometric equivalent of oxygen uptake to sediment decay) should be near the 6-25 °C range.

#### DOMT1, DOMT2

- 128. DOMT1, the critical low temperature for DOM decay, is usually 0 °C.
- 129. DOMT2 is the optimum temperature for DOM decay (°C). Temperature coefficients for DOM decay are given in Table 38.

Table 38

Temperature coefficients for DOM decay (°C)

| SUBSTRATE                          | DOMT1  | DOMT2       | REFERENCE                      |
|------------------------------------|--------|-------------|--------------------------------|
| Glucose<br>Glucose: Lake           | 5.0    | 35.5        | Toerien and Cavari 1982        |
| George, N.Y. Glucose Glucose: Lake | 0<br>0 | 25<br>20-30 | Tison et al. 1980<br>Bott 1975 |
| Wingra, Wis.                       | 0      | 25-30       | Boylen and Brock 1973          |

## NH3T1, NH3T2

- 130. Researchers have generally found temperature to affect nitrification rates, especially in the range of 10 to 35  $^{\circ}\text{C}$ .
  - a. NH3T1 is the lower temperature boundary at which ammonium nitrification continues. It is generally 0 °C.
  - b. NH3T2 is the optimum temperature for oxidation of NH3-N. The optimum temperature for nitrification is generally accepted to be between 25 and 30 °C.

Temperature factors for ammonia oxidation are given in Table 39.

Table 39

<u>Temperature coefficients for ammonia oxidation (°C)</u>

| SPECIES OR SITE                      | NH3T1  | NH3T2    | REFERENCE                          |
|--------------------------------------|--------|----------|------------------------------------|
| Nitrosomonas<br>Wastewater treatment | 5      | 30       | Knowles et al. 1965                |
| plant<br>Ann Arbor, Michigan         | 5<br>2 | 25<br>20 | Wild et al. 1971<br>Borchardt 1966 |

## NO2T1, NO2T2

- 131. NO2T1 is the lower temperature boundary at which nitrate nitrification occurs (°C).
- 132. NO2T2 is the lowest temperature (°C) at which the oxidation of nitrite to nitrate occurs near the maximum rate.

## TSSETL

133. TSSETL is the suspended solids settling velocity (m/day). The settling rate is dependent on the type of particle, grain size, density, temperature, viscosity, and turbulence. Most of the larger particles entering a reservoir settle very quickly and should not be included in the inflow. Lane (1938) gives figures of 0.86 to 860.0 m/day for particle diameters of 0.002 to 0.1 mm. Particles found in the main body of a reservoir are usually at the lower end of this scale.

## QlocoL

134. CE-QUAL-Rl uses a Ql0 formulation to modify the coliform die-off rate as a function of temperature. All other rates are modified by temperature through the RMULT function in CE-QUAL-Rl. The Ql0 coefficient is usually 1.04.

# PART III: RECOMMENDATIONS

- 135. This report provides information about, and values for, many of the coefficients needed for use of the version of the model CE-QUAL-R1 described in the User's Manual (Environmental Laboratory 1982).
- 136. Research on processes described in this report is likely to provide more information needed to refine the equations used in the model. Future versions of the model may therefore require additional coefficients.
- 137. This report may be updated to provide information about, and values for, any additional coefficients needed for use of future versions of the model.
- 138. Application, calibration, and verification of the model to a variety of sites is likely to identify coefficient values that are best suited to the model. These values may be included in updates to this report.

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